



Simulating personal future events: Contributions from episodic memory and beyond

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Simulating personal future events:
Contributions from episodic memory and beyond

A dissertation presented

by

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to

The Department of Psychology

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Abstract

Episodic simulation refers to the construction of imagined, hypothetical events that might occur in one's personal future. Damage to our capacity for episodic simulation can produce grave consequences, impairing our ability to anticipate, plan, and prepare for the future. New theoretical approaches have begun to uncover the cognitive and neural mechanisms underlying episodic simulation, but much remains to be examined. The purpose of this dissertation is to further investigate the mechanisms supporting episodic simulation as well as the functions it serves. In the first study of the dissertation I examine age-related deficits in imagining the future, remembering the past, and describing the present (Paper 1). These findings replicate known deficits in older adults in episodic simulation and memory, yet provide evidence of non-episodic processes that also shape their expression. I next examine component cognitive and neural processes that are recruited to generate imagined events (Paper 2). Distinct regions of the hippocampus were active when encoding, tracking novelty, or constructing imagined events, suggesting a multifaceted role of the hippocampus in supporting episodic simulation. Finally, I present evidence that episodic simulation and memory can be used to facilitate empathy, that is, intentions to help a person in need (Paper 3). People are more willing to help a person in need after imagining or remembering helping that individual. Furthermore, the episodic vividness of these imagined or remembered events heightened intentions to help. These findings elucidate a previously unconsidered mechanism for facilitating empathy, and, in doing so, open the possibility for a new functional account of episodic simulation. I close by discussing the promise

of this line of work that aims to provide new insights into the relationship between episodic simulation, memory, and empathy.

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Introduction

Consider the following scenario: While beginning to read this dissertation, the floor drops out and you are whisked away in a secret tunnel designed by mad scientists. Taken to a subterranean laboratory, the mad scientists use a sophisticated machine to selectively remove all your memories of past experiences before returning you to the world above. The consequences of losing your ability to remember the past would be devastating. Strip away your memory, and all that you hold familiar would become alien and distant. Unable to remember what you were thinking moments ago, your career would unravel, family members would appear as strangers, the love of your life would seem drained of intimacy, your sense of personal identity would mutate. But it gets worse. Strip away your memory, and you would likely be unable to effectively plan and carry out actions in the future. Investing for your retirement would appear nonsensical, intentions to stay in touch with friends would go unrealized, preparations for the arrival of your newborn would be muddled at best, your future would be dim. Unanchored in time and place, you would be adrift in an endless sea of the present. Although mad scientists running amok erasing memories is fiction, the consequences in everyday life of losing memory—and losing your ability to imagine hypothetical future events as a result—are very real.

Researchers studying memory have long understood the importance of remembering the past, but we have only recently begun to discover the importance of imagining the future and its close relationship to memory (Atance & O'Neill, 2001; Buckner & Carroll, 2007; Ingvar, 1979, 1985; Hassabis & Maguire, 2007; Gaesser, 2013; Schacter, Addis, & Buckner, 2007; Schacter, 2012; Suddendorf & Corballis, 1997, 2007; Szpunar, 2010; Tulving, 2002). Deficits in remembering past events, previously observed across a wide array of neurological and psychiatric disorders, have recently been extended to deficits in imagining the future in these

disorders, including Alzheimer's disease (Addis, Sacchetti, Ally, Budson, & Schacter, 2009), amnesic mild cognitive impairment (Gamboz et al., 2010), amnesia (Hassabis, Kumaran, Vann, & Maguire, 2007; Klein, Loftus, & Kihlstrom, 2002; Tulving, 1985), depression (Williams et al., 1996), post-traumatic stress disorder (Brown et al., 2013), schizophrenia (D'Argembeau, Raffard, & Van der Linden, 2008), and traumatic brain injury (Rasmussen & Berntsen, in press).

While more accurately characterizing and improving deficits in imagining events is an important objective for developing therapies to address these mental disorders, understanding the nature of imagined future events also has implications for healthy individuals. For college students, imagining the steps they need to take to study for an impending exam can help them to better prepare for—and perform on—the exam (Taylor, Pham, Rifkin, & Armor, 1998). Older adults, who report fewer episodic details for imagined future events than do young adults, also produce fewer means of effectively solving everyday problems (e.g., moving into a new neighborhood, finding a lost watch; Sheldon, McAndrews, & Moscovitch, 2011). Imagining future events has even been shown to promote less impulsive and more farsighted decision-making: imagining receiving a reward in the future attenuated a bias toward selecting more immediate but less valuable rewards, in contrast to merely viewing the reward amount and delay (Peters & Büchel, 2010), or generating semantic estimates of what the reward could be used to purchase (Benoit, Gilbert, & Burgess, 2011). Indeed, the number of known useful functions in everyday life supported by imagining the future is rapidly growing (Gerlach, Spreng, Gilmore, & Schacter, 2011; Gollwitzer, 1999; Hassabis & Maguire, 2007; Klein, Robertson, & Delton, 2010, 2011; Schacter, 2012; Schacter et al., 2012; Suddendorf & Corballis, 2007; Szpunar, 2010). Coupled with the growing evidence for a link between remembering the past and imagining the

future, the landscape of memory research has started to shift, with increased emphasis on the role of memory in supporting future imaginings.

Amidst this shifting landscape lies this dissertation. I will begin by reviewing the general background and theoretical framework that unites my work (Papers 1-3). I will then consider the literature specifically motivating each paper. After presenting each paper, I will then discuss the broader theoretical, clinical, and applied significance of this dissertation. In closing, I will highlight a few outstanding questions that arise from this dissertation, and what I believe will be exciting and productive directions for research moving forward.

Remembering the past to imagine the future: The relationship between episodic memory and episodic simulation

The main emphasis in research on memory is largely focused on identifying the mechanisms of encoding, storage, and retrieval (Ezzyat & Davachi, 2011; Gold et al., 2006; Johnson, McDuff, Rugg, & Norman, 2009; Liang, Wagner, & Preston, 2013). This mechanistic approach has been highly informative, but it leaves unexplained questions regarding the function of memory. Fortunately, progress is starting to be made on this front. Partially addressing questions concerning adaptive function, researchers have recently begun to examine a key benefit of memory deriving from its role in building simulations of hypothetical events set in the future. Much of this work has focused on the contributions of remembering specific past events (i.e., *episodic memory*; Tulving, 1972, 1983, 2002) to building such simulations. Throughout this dissertation, I will use the term *episodic simulation* to refer to the *imaginative construction of hypothetical events in one's personal future*, in line with previous usage (Schacter, Addis, & Buckner, 2008; Taylor & Schneider, 1989). It is worth noting that episodic simulation is part of a broader category, 'mental simulation', which involves disengaging from the external

environment in order to mentally project into hypothetical experiences (Buckner & Carroll, 2007; Morewedge, Gilbert, & Wilson, 2005; Spreng, Mar, & Kim, 2009). However, compared to other forms of mental simulation (e.g., perspective taking, spatial navigation), episodic simulation uniquely involves a constellation of personal details set in a specific time and place. Critically, mounting evidence indicates that episodic memory and episodic simulation depend, to a strikingly large extent, on shared cognitive and neural processes.

Evidence supporting shared processing draws from a variety of empirical approaches. Studies from cognitive psychology demonstrate similar subjective experiences of past and future events for experimental manipulations of contextual vividness (e.g., imagining an event in a familiar setting compared to an unfamiliar setting; Szpunar & McDermott, 2008), emotional valence and temporal distance from the present (D'Argembeau & Van der Linden, 2004; Spreng & Levine, 2006), and individual differences in emotion regulation strategies, imagery, and self-defining features important for supporting self-identity (D'Argembeau & Van der Linden, 2006; D'Argembeau, Lardi, & Van der Linden, 2012). The most revealing neuropsychological evidence comes from studies on amnesic patients with damage to the hippocampus and related structures. Beyond deficits in episodic memory, mounting evidence suggests these patients also show impoverished imagination (Hassabis, Kumaran, Vann, et al., 2007; Klein et al., 2002; Race, Keane, & Verfaellie, 2011; Tulving, 1985). Typically, amnesic patients in these studies are able to imagine some aspects of personal events, but the phenomenology of the simulations is impaired, leading to events with attenuated specificity, vividness, and spatial coherence. Hassabis and colleagues (2007) offer evidence of a particularly strong coupling between episodic memory and imagination, since the lesions appear to be confined to the hippocampal formation. In their study, amnesic patients experienced difficulty constructing imaginary scenes (e.g.,

imagining lying on a white sandy beach): their imagined scenes contained less content, and the content that was generated was less coherent compared to healthy controls (Hassabis, Kumaran, Vann, et al., 2007). Although Squire et al. (2010) reasoned that the clinical profiles of these patients (e.g., generalized atrophy and seizures) reflect damage outside of the hippocampus, Maguire & Hassabis (2011) argued against this interpretation, since the patients performed normally on neuropsychological tests (except on tests of memory) and were selected specifically for their lesions restricted to the hippocampus. Recently, however, there is some evidence that a fully intact hippocampus may not be necessary for episodic simulation. One group of amnesic patients with bilateral hippocampal damage but spared remote memories (Squire et al., 2010), an adult developmental amnesic patient (Maguire, Vargha-Khadem, & Hassabis, 2010), and children with developmental amnesia (Cooper, Vargha-Khadem, Gadian, & Maguire, 2011) can construct imaginary scenarios. Notably, these results emerged from the scene construction task (Hassabis, Kumaran, Vann, et al., 2007), a task that does not strictly require mental time travel into the past or future per se, but rather requires participants to merely imagine novel experiences in a particular setting (e.g., on a beach, in a museum). These ostensibly conflicting findings leave the role of the hippocampus in episodic simulation open for debate, and raise the possibility that distinct regions of the hippocampus support different aspects of simulation. For example, one possibility is that distinct hippocampal regions support retrieving details from memory, recombining these details into coherent events, and encoding these scenarios into memory for use in the future. Thus, depending on the lesion site of the hippocampus, different component processes of episodic simulation may be differentially affected (Addis & Schacter, 2012; Martin, Schacter, Corballis, & Addis, 2011). Neuroimaging research consistently finds a common neural network that substantially overlaps with the default network (Andrews-Hanna, 2012; Buckner,

Andrews-Hanna, & Schacter, 2008; Raichle et al., 2001)—notably, the medial prefrontal and parietal cortex, medial temporal lobes (including hippocampus), lateral temporal and parietal cortex—underlies remembering past events, imagining future events, and associated forms of simulation (Addis, Wong, & Schacter, 2007; Addis, Roberts, & Schacter, 2011; Okuda et al., 2003; Spreng et al., 2009; Szpunar, Watson, & McDermott, 2007; for reviews, see Buckner & Carroll, 2007; Schacter et al., 2012; Szpunar, 2010).

These converging findings from behavioral, neuropsychological, and neuroimaging studies form the basis of the *constructive episodic simulation hypothesis* (Addis & Schacter, 2012; Schacter & Addis 2007, 2009). The *constructive episodic simulation hypothesis* proposes to explain the shared network for remembering and imagining by contending that episodic memories are the raw materials for episodic simulations, and that the flexible nature of memory, which renders it vulnerable to false memories, also underlies the recombination of episodic details into novel simulations that can be used to adaptively guide future behavior.

Episodic memory is flexible: a re-construction of past events rather than a verbatim reproduction (Bartlett, 1932; Johnson, Suengas, Foley, & Raye, 1988; Loftus & Palmer, 1974; Schacter, 1999). Such a flexible system is prone to error, such that people sometimes remember experiences that never actually happened (Loftus, 2003). Memory researchers have paid close attention to understanding how these errors arise, and for good reason, given the everyday consequences of misidentifying a suspect during eyewitness testimony (Loftus, 2005). Yet, despite the cost of this flexible, constructive system in sometimes producing distortions, errors, and biases, according to the constructive episodic simulation hypothesis, it also is thought to support an adaptive process: the ability to imagine novel hypothetical future events (i.e., episodic simulation).

Episodic simulation is proposed to rely on many of the same cognitive processes as episodic memory. In particular, disparate details can be gleaned across remembered past events and re-constructed into a novel representation of an imagined future event. This constructive system has adaptive benefits for planning and prediction with an emphasis on the benefit of enhancing decision-making between alternative choices in novel situations (see Schacter, 2012, for a comprehensive review). By simulating possible future events, we can mentally “try out” alternative hypothetical scenarios of what might happen, contemplate the outcomes of selecting different actions, and winnow our options down to the preferred course of action. Thus, imagining hypothetical future events can be used to inform prediction and planning while saving the costs of engaging in physical behavior. Physically acting out each hypothetical scenario would be exhaustive, cumbersome, and in some cases impossible; for instance, selecting one lover over another affords little opportunity to “test” alternative options. Whether hunting for a new job, anticipating the arrival of a newborn, or preparing for retirement, the mental flexibility to “try out” novel events by imagining the potential outcomes of different actions is thought to help guide future decision-making (Buckner & Carroll, 2007; Ingvar, 1979; Schacter & Addis, 2007, 2009; Schacter et al., 2008; Suddendorf & Corballis, 2007; Tulving, 2005).

Consistent with this theoretical framework, while both remembering the past and imagining the future draw on many of the same cognitive processes, important differences are also beginning to emerge (see Schacter et al., 2012 for review). Most notably, additional cognitive resources have been proposed to support episodic simulation compared with episodic remembering. Since imagining future events is thought to involve recombining more disparate details from across experiences than remembering, more intensive constructive (or relational)

processing is required to bind and integrate such details into a coherent simulation (Addis & Schacter, 2012).

Building on the foundational studies and theoretical approach above, this dissertation consists of three papers that distinguish the contributions of episodic memory from non-episodic processes to imagining future events in order to gain a better understanding of the nature of episodic simulation, the processes that shape its expression, and the function it serves. Specifically, the papers in this dissertation aim to characterize the episodic deficits in older adults (Paper 1), delineate intrinsically related processes recruited for imagining future events (Paper 2), and explore a novel function of episodic simulation in facilitating prosocial intentions (Paper 3).

Paper 1: Aging and episodic simulation

Research motivated by the constructive episodic simulation hypothesis has recently examined episodic simulation and episodic memory in cognitive aging. As people age, episodic memory declines in various ways (e.g., Craik & Salthouse, 2000). Many studies have documented age-related deficits using word lists or similar materials encoded in the laboratory, while less work has investigated the finding that older adults also provide less specific memories of past experiences for everyday events compared to young adults. Supporting evidence for this point has been provided by research using the Autobiographical Interview (AI) (Levine, Svoboda, Hay, Wincour, & Moscovitch, 2002). For the AI protocol, older and younger adults recalled specific personal past events in response to probes concerning different periods over the lifespan (e.g., events from early childhood to events from the previous year). Subjects were provided with 5 minutes to recall individual experiences, and their descriptions of the events were transcribed and then segmented into episodic or “internal” details (e.g., who, what, when,

and where details) and “external” details (e.g., semantic information, other external events, repetitions). Levine et al. (2002) showed that the episodic specificity of older adults’ autobiographical memories was impoverished compared with those provided by young adult; older adults produced fewer internal and more external details during the AI than did young adults.

A natural question that arises in response to these findings from the perspective of the constructive episodic simulation hypothesis is whether or not the reduced episodic specificity for remembered past events would extend to imagined future events. Since the hypothesis specifies a large degree of overlap between the processes supporting episodic memory and episodic simulation, it predicts a similar age-related decline in episodic specificity for imagined future events.

Addis, Wong, and Schacter (2008) evaluated this hypothesis using an adapted version of the AI. In their study, older and young adults remembered or imagined events in response to word cues, generating as much detail as possible within three minutes. Replicating the findings of Levine et al. (2002), older adults produced fewer internal and more external details than young adults for remembered past events. Critically, the same pattern was observed for imagined future events. These results and those of a follow-up study that yielded similar results with a different experimental paradigm (Addis, Musicaro, Pan, & Schacter, 2010) are consistent with the constructive episodic simulation hypothesis; however, since the AI consists of generating narratives (i.e., verbal reports about experiences), the age-related differences in memory and imagination could be explained by deficits in a number of non-episodic processes related to the production of narrative discourse. This possibility is especially a concern because the linguistics literature has shown that older adults often possess different narrative goals and produce more

off-topic speech than do younger adults (James, Burke, Austin, & Hulme, 1998; Schacter, Gaesser, & Addis, 2010, 2013; Trunk & Abrams, 2009). Differences in narrative style could account for changes in specificity if older adults possess different communicative goals than young adults, focusing on personal meaning rather than exact recapitulation of details (Arbuckle & Gold, 1993, Coupland & Coupland, 1995). Another possible explanation is that a general decline in the ability to inhibit task-irrelevant thought leads to older adults generating more off-topic details (Zacks & Hasher, 1994). Although Paper 1 of this thesis proposal was not designed to directly distinguish between these non-episodic processes, it does attempt to distinguish more broadly between episodic and non-episodic contributions to remembering and imagining personal events. In two experiments, Paper 1 evaluates whether the detail deficits observed for episodic simulation and episodic memory extend to descriptions (i.e., verbal reports) of pictures for everyday scenes—a task that does not explicitly rely on episodic memory processes, since the picture is presented in front of the participant for the duration of the trial. The constructive episodic simulation hypothesis predicts that age-related deficits in episodic simulation and memory will be attributed to impairments in episodic processes. In other words, picture description performance associated with broader non-episodic factors such as descriptive ability or communicative goals will not fully account for age-related differences in episodic simulation and memory. Alternatively, age-related differences may reflect the operation of these non-episodic factors. As described in Paper 1, this line of work stands to provide a greater understanding of age-related decline in episodic simulation and memory of healthy older adults and has implications for better characterizing and improving deficits in pathological older adults, beginning to reveal the link between episodic processes and higher-order non-episodic factors that shape its expression.

Paper 2: Component processes of episodic simulation

Paper 2, like Paper 1, reports an attempt to gain a better understanding of the underlying cognitive processes that support episodic simulation. However, whereas Paper 1 examines the shared cognitive processes between episodic simulation and episodic memory using behavioral methods, Paper 2 investigates processes that are preferentially recruited for episodic simulation using functional MRI.

Although episodic simulation and episodic memory rely on a strikingly similar network of brain regions, several regions within this network (including the hippocampus) have consistently shown greater activity for imagining future events compared to remembering past events. Particularly puzzling for researchers has been interpreting activity in the hippocampus that is greater for imagining compared to remembering, because this region is traditionally considered to fundamentally support episodic memory (see Addis & Schacter, 2012 for review). One explanation for this pattern of results is that the simulation-preferential hippocampal activation reflects more intensive constructive processing, that is, recombining details gleaned across disparate episodic memories into a coherent novel scenario (Schacter & Addis, 2007). According to this view, while both episodic simulation and episodic memory require the retrieval of stored details, imagination involves the additional process of flexibly integrating details into a novel scenario.

Supporting evidence comes from studies that have observed greater hippocampal activity when the degree of constructive processing is increased by appropriate experimental manipulations. For example, Weiler, Suchan, and Daum (2010) observed greater hippocampal activity when subjects imagined future events that had a lower probability of occurring compared to a higher probability. Lower probability events are thought to require greater recombinatory

processing, since lower probability events involve increased demands to bind together disparate details than do high probability events that have already been planned. Similarly, Addis and Schacter (2008) showed activity in the hippocampus that was preferentially driven by degree of imagined detail: the more detailed an imagined event was, the greater the hippocampal activity. Furthermore, constructing more episodic (specific) future events, compared to general (routine) future events, also increased hippocampal activity. The former task requires greater recombination of episodic details relative to the latter task, which draws more on conceptual knowledge (Addis, Cheng, Roberts, & Schacter, 2011). Such convergent findings suggest that the disruption of the hippocampus may engender deficits in imagining future events. Findings from neuropsychological patients lend some support to this hypothesis.

As noted earlier, amnesic patients have been reported with impaired ability to imagine coherent scenes and future events (Tulving, 1985; Klein et al., 2002, Hassibis, Kumaran, Vann, et al., 2007; Race et al., 2011). Patient K. C. exhibited dense autobiographical amnesia that extended to an inability to imagine specific future events (Tulving, 1985). Patient D. B. also exhibited a parallel deficit across memory and simulation, unable to remember or imagine personal events (Klein et al., 2002). Extra-hippocampal damage is known to exist in patient K.C. and may exist in patient D.B., and so strong claims regarding the role of the hippocampus and function it serves cannot be discerned from these patients alone. More recent work, however, has attempted to focus on patients with damage thought to be restricted to the hippocampus. For example, Hassabis et al. (2007) found that four out of five amnesic patients produced significantly less content when imagining scenarios of everyday scenes compared to healthy controls (e.g., lying on a beach, standing in a museum).

Although the selectivity of lesions in these patients has been called into question based on the patients' clinical profiles (Squire et al., 2010), other researchers have observed evidence consistent with the notion that damage to the hippocampus and episodic memory retrieval is sufficient to disrupt episodic simulation. For instance, the one patient from a study by Race et al. (2011) who had confirmed damage restricted to the hippocampus was similarly impaired when imagining future events compared to patients with extra-hippocampal temporal lobe damage. Although a number of cases of developmental amnesic patients with a relatively preserved ability to imagine events have been documented (Maguire et al., 2010; Hurley, Maguire, & Vargha-Khadem, 2011; Cooper et al., 2011), these patients incurred damage early in life. Consequently, it is possible that they developed compensatory strategies to generate imagined scenarios. Overall, these findings are beginning to establish a consensus that memory retrieval fundamentally underlies episodic simulation. Without the ability retrieve past events, people are unable to use episodic details as building blocks to assemble imagined future event. Less agreement has been reached concerning the role of the hippocampus in supporting a flexible recombination process.

If the hippocampus' contribution to episodic simulation supports a recombination process in addition to memory retrieval, then one would not expect cases of patients with damage to the hippocampus and a preserved ability to imagine coherent future events. However, patients with selective memory impairments capable of imagining future events have recently been observed. Squire et al. (2010) examined a group of patients with damage circumscribed to the hippocampus. These patients exhibited a minimal degree of retrograde amnesia with a seemingly preserved ability to imagine detailed future events (but see Andelman, Hoofen, Goldberg, Aizenstein, & Neufeld, 2010). Since these patients could retrieve remote past events and only

showed mild (non-significant) deficits in recent past events, these results could be viewed as supporting the idea that retrieval of past events is necessary for imagining novel events. The results also suggest that access to the past is sufficient to account for the role of the hippocampus in imagining events and there is no need to evoke the additional process of recombination in order to generate coherent and meaningful scenarios. What is to be made of these inconsistencies in the literature?

One way of reconciling the discrepancies across neuroimaging and patient studies is if distinct regions within the hippocampus support separate component processes underlying episodic simulation (Addis & Schacter, 2012). This multifaceted account proposes that the hippocampus supports three distinct—but related—processes that contribute to imagining future events: retrieving episodic details, recombining details into coherent and meaningful scenarios, and encoding the newly formed scenarios to help guide future decision making. In this way, damage to one aspect of the hippocampus could leave the other processes intact thereby giving rise to differential patterns of impairment in hippocampal patients depending on the location of the damage. Elucidating the precise contribution of episodic memory to episodic simulation requires teasing apart these related component processes.

It may be particularly difficult to isolate a constructive recombination process from processes related to encoding novel events, because the functional utility of imagining future events is to imagine *novel* events that a person has not already experienced. Thus, previous comparisons of episodic memory and episodic simulation were confounded by associative novelty. That is, retrieving disparate episodic details into a new combination entails more novel associations compared to retrieving details that were previously associated within an episode. Given the known role of the hippocampus in encoding novel events (e.g., Schacter & Wagner,

1999) and novelty detection (e.g., Kumaran & Maguire, 2007), the imagination-preferential hippocampal activity may in fact reflect novelty-related processing rather than detail recombination. Consistent with this possibility, Addis et al. (2011) found that specific future events, which were thought to involve more constructive processing than general future events, also contained higher levels of subjective novelty; this confounding of constructive processing and novelty made it difficult to attribute hippocampal activity in that study to either recombination or novelty per se. Further weakening the notion of a hippocampal recombination process, a recent study by Martin et al. (2011) found that the activity of regions in the hippocampus that had previously shown an imagination-greater-than-memory effect was directly modulated by subsequent memory performance. However, there was some evidence of a recombination-specific process, in that the pattern of functional connectivity between the hippocampus and other default network regions suggested hippocampus activity could not be fully accounted for by encoding effects. What is needed, then, is a means of independently manipulating encoding and recombination processes while controlling for novelty-related processing. Currently, it remains an open question as to which specific component processes drive activity in the hippocampus during episodic simulation. An issue of considerable theoretical importance is whether the hippocampus underlies a recombination process that supports imagining future events, or whether only processes such as encoding and novelty detection are preferentially engaged by imagining compared to remembering. To isolate the contributions of the hippocampus to imagining future events, in Paper 2 we drew on experimental recombination (Addis, Pan, Vu, Laiser, & Schacter, 2009), subsequent memory (Wagner et al., 1998), and task switching paradigms (Duncan, Ketz, Inati, & Davachi, 2012) in order to build a comprehensive experimental procedure that allows us to systematically tease

apart a constructive recombination process from alternative interpretations of hippocampal activity observed during episodic simulation (i.e., encoding novel experiences, detecting changes in the environment).

Paper 3: Constructing empathic events

Papers 1 and 2 both aim to identify and delineate aspects of the cognitive architecture supporting episodic simulation. Paper 3 takes a slightly different approach. Rather than focus on the underlying mechanisms, Paper 3 investigates how these mechanisms can be leveraged in a social decision-making context, and, in doing so, explores a previously unconsidered function of episodic simulation: facilitating prosocial intentions to help others.

Empathy—a willingness or intention to help others—and prosocial behavior are hallmarks of our species and essential for mental health (Melis & Semman, 2010; Nowak & Highfield, 2011; Rand, Green, & Nowak, 2012; Wilson, 2000; Zaki & Ochsner, 2012). Empathy is a multifaceted construct used to describe a variety of concepts in psychology and neuroscience. The prominent social psychologist Daniel Batson (2011) acknowledged no less than seven different uses of the term “empathy”, including accurately perceiving another person’s internal state (de Waal 1996; Premack & Woodruff, 1978; Tomasello & Call, 1997), projecting what another person is thinking and feeling (i.e., perspective taking; Batson, Early, & Salvarani, 1997; Davis, 1994; Stotland, 1969), and feeling distress at witnessing another person’s suffering (Piliavin, Dovidio, Gaertner, & Clark, 1981; Hoffman, 1981). Although providing an in-depth review of each of these uses is beyond the scope of this dissertation, I mention them so as to explicitly (i) recognize diversity and complexity in the field, (ii), acknowledge that these states—although distinct—could interact, and (iii) clarify my own use of the term by contrast.

Accordingly, in this dissertation I use the term “empathy” to mean a prosocial motivation or intention to help others (Zaki & Ochsner, 2012).

While our capacity to work with and help others in need is a central aspect of human social life (Adolphs, 1999; Dunbar, 1998; Rand et al., 2012; Nowak & Highfield, 2011), instances of empathic failure also abound (Cikara, Bruneau, & Saxe, 2011). This failure is particularly evident when the people in need are from stigmatized groups (e.g., the diseased or destitute) or are competitors (Batson, Polycarpou, et al., 1997; Batson, Chang, & Rowland, 2002; Epley, Caruso, & Bazerman, 2006). Social psychologists and neuroscientists have largely emphasized how adopting the thoughts and feelings (i.e., perspective-taking, akin to mentalizing and theory of mind) of the person in need supports our prosocial tendencies (Batson, Early, et al., 1997; Coke, Batson, & McDavis, 1978; Decety, 2005; Mathur, Harada, Lipke, & Chiao, 2010; Waytz, Zaki, & Mitchell, 2012). Much of this research suggests that adopting the perspective of a person in need may heighten our awareness of his pain and suffering, eliciting emotional concern that then prompts us to help. Little attention, however, has been given to the potential impact of episodic simulation and memory on empathic responses (see Gaesser, 2013 for review). Are people more willing to lend a helping hand when they imagine doing so in the future (i.e., episodic simulation) or when they remember doing so in the past (i.e., episodic memory)?

Determining willingness to help in any meaningful sense requires a person to reflect on the perceived probability that he or she will act. Currently there is no direct evidence for the impact of episodic processes on empathy. However, there is relevant work from the memory and social judgment literatures that offers some insight. In reaction to the controversy on the veracity of traumatic memories recovered during therapy that employed guided imagery techniques,

researchers began investigating the effect of imagining on memory distortion (Garry & Polaschek, 2000). These studies on *imagination inflation* showed that imagining a novel event increases the perceived likelihood that it occurred in one's past, and in some cases produces "implanted" rich false memories of events that never happened (Hyman & Pentland, 1996; Mazzoni & Memon, 2003). In one illustrative study, subjects rated how confident they were that a list of possible childhood events had occurred, imagined a subset of these events two weeks later, and were then asked to re-rate their confidence that the childhood events occurred under the guise that the researcher had misplaced the original ratings (Garry, Manning, Loftus, & Sherman, 1996). Subjects' confidence ratings that an event had occurred in their personal pasts were inflated after imagining an experience compared with a non-imagined experience. This line of research suggests that imagining events can impact the perceived probability that an event occurred in the past, but if the power of imagining is to be harnessed to increase prosociality, then its impact will need to run in the other temporal direction: the future.

Social psychologists have studied how imagining hypothetical experiences increases the perceived probability that the experience will occur in the future (Anderson, 1983; Carroll, 1978; Greenwald, Carnot, Beach, & Young, 1987; Sherman, Cialdini, Schwartzman, & Reynolds, 1985). Typically, memory distortion researchers view the consequences of imagination inflation as harmful, yet this approach was partially informed by studies on prediction in social judgment that elucidated more benign effects of imagining events. Investigating decision-making heuristics, Carroll (1978) initially documented the influence of imagined events on predictions, finding that imagining events related to a presidential victory increased the likelihood that the imagined victor would win. Importantly, the impact of imagining events has also been extended to *actual* voting behavior (Libby, Shaeffer, Eibach, & Slemmer, 2007), and in some cases, can

predict behavioral effects two to three months after initially imagining an experience (Gregory, Cialdini, & Carpenter, 1982).

More recent work from memory researchers has shown that repeatedly imagining an emotional event increases estimates of the perceived plausibility that the imagined event will occur in the future (Szpunar & Schacter, 2013). Although the effect of episodic simulation on helping an individual in need has not been examined, several studies have used imagination to promote socially desirable attitudes and behaviors, including reducing dropout rates for clinical treatment (Sherman & Anderson, 1987) and increasing intentions to donate blood (Anderson, 1983; Armitage & Reidy, 2008)

Further evidence suggesting that imagined events could be used to facilitate prosocial intentions comes from work on intergroup interactions. Although empathy is pervasive, when the suffering person is from a social, racial, or cultural outgroup, empathy can be reduced or absent (Cikara et al., 2011). One of the most effective techniques for attenuating outgroup bias has been positive intergroup contact. Under the right conditions, contact between members from different groups lessens intergroup hostility and prejudice while heightening positive intergroup attitudes (Allport, 1954; Pettigrew & Tropp, 2006). Although contact with outgroup members may be ideal for attenuating outgroup bias, it has practical limitations. Namely, the opportunity for face-to-face contact may be unavailable where it is needed the most, as is the case for highly segregated groups. But does the outgroup member need to be physically present to improve intergroup attitudes, or might this hurdle be overcome by merely imagining contact with outgroup members? Recent research suggests that the prosocial benefits of contact can also be reaped through imagined social contact. Imagining a positive social interaction with an outgroup

member can improve intergroup attitudes and reduce prejudice (Crisp & Turner, 2009; Turner, Crisp, & Lambert, 2007).

Although a useful tool for flexibly improving intergroup relations, imagined contact is unlikely to be as effective as person-to-person contact (Turner et al., 2007), as direct experiences produce stronger attitudes than indirect experiences (e.g. Fazio, Powell, & Herr, 1983). One plausible explanation for this difference may be that knowledge accessed through perception is more cognitively available compared to knowledge accessed through imagined events (Tversky & Kahneman, 1973). As an imagined event more closely resembles perception (i.e., is more vivid in the mind's eye), the event is brought to mind more easily, and thereby more strongly weighted as diagnostic knowledge that guides judgments of event plausibility (Anderson, 1983; Crisp, Husnu, Meleady, Stathi, & Turner, 2010).

Would increasing the vividness of an imagined intergroup interaction enhance intentions to interact with outgroup members? Indeed, previous research on intergroup contact has shown that instructing participants to imagine specifically *when* and *where* they would positively interact with unfamiliar others led to greater intentions to interact with unfamiliar others (Husnu & Crisp, 2010). Notably, specific temporal (*when*) and contextual (*where*) contexts represent two defining features of episodic experiences (Tulving, 2002). Furthermore, vividness predicted willingness to interact, independent of changes in attitude and anxiety. As the vividness of an imagined event increased, people were more willing to interact with others.

Although my focus has been on discussing relevant behavioral studies that point to a possible effect of episodic processes on empathy, I will briefly note some relevant—though more tentative—work from neuroscience. The neuroscience of episodic memory and simulation on the one hand, and empathy on the other, have mostly advanced in parallel with little intersection

between these two lines of investigation. However, evidence across experiments indicates there may be overlap between the brain networks that support episodic processes and empathy (Gaesser, 2013). To the degree that specific cognitive faculties can be localized to particular brain regions (Henson, 2005), this overlap reflects contributions of one cognitive process to another (e.g. episodic processes informing empathic processes) or component processes recruited across cognitive processes (e.g. self-referential processing recruited for both episodic processes and empathy). Co-morbid deficits in episodic processes and empathy have been observed in patient populations such as those with autism spectrum disorder (Lombardo, Barnes, Wheelwright, & Baron-Cohen, 2007) and schizophrenia (Corcoran & Frith, 2003; Lee, Farrow, Spence, & Woodruff, 2004), consistent with the notion that episodic memory and simulation may contribute to supporting empathy.

Evidence from neuroimaging studies also points to a possible neural overlap between episodic processes and empathy. Several of the same brain regions forming a common core network (commonly referred to as the default network) that supports remembering past events and imagining future events and related processes are also recruited during tasks that elicit empathy (Andrews-Hanna, 2012; Buckner et al., 2008; Mitchell, 2009; Schacter et al., 2012). In particular, activity in the precuneus and medial prefrontal cortex has been shown to be preferentially recruited when observing a person in need (Masten, Morelli, & Eisenberger, 2011; Mathur et al., 2010). And, in some cases, activity in these regions has even predicted prosocial behavior (Masten et al., 2011; Rameson, Morelli, & Lieberman, 2012; Waytz et al., 2012). Because similar regions are activated when remembering and imagining, an intriguing possibility is that episodic processes could affect empathy through these same neural mechanisms (e.g., self-

referential processing)—though such interpretive logic should be met with caution in the absence of direct empirical investigation.

Perhaps the most tantalizing neuroscience data consistent with a link between episodic processes and empathy comes from a study showing empathic deficits in amnesic patients (Beadle, Tranel, Cohen, & Duff, 2013). Amnesic patients, suffering damage to the medial temporal lobe, displayed lower levels of trait empathy, were less responsive to empathy inductions, and were less prosocial in a social-economic context (e.g., the Dictator Game) compared to healthy controls. The authors of this study interpreted these empathic deficits as evidence that retrieving past events contributes to inferring the mental states of another person (i.e., perspective taking), similar to previous interpretations of the relationship between memory and social cognition (Rabin & Rosenbaum, 2012; Perry, Hendler, & Shamay-Tsoory, 2011). This account proposes that recalling past experiences can serve as a guide in predicting the mental state of another person, which in turn promotes empathy. Thus, in this way, the effect of episodic processes on empathy is thought to be mediated by perspective taking. However, an alternative interpretation is that accessing episodic representations directly affects judgments in social decision-making context rather than being mediated by theory of mind or perspective taking by serving as diagnostic knowledge that guides judgments about future actions to help. At present, the underlying cognitive mechanisms remain obscure. Nevertheless, when taken as a whole, the findings from imagination inflation, imagined intergroup contact, and social neuroscience literatures suggest episodic processes could be used to facilitate empathy.

To begin to investigate a possible effect of episodic processes on empathy, I developed and ran three experiments in my last year of graduate school using a novel paradigm that combines a theoretical approach and manipulations from cognitive psychology with dependent

measures from social psychology (Paper 3). Previous work has suggested that the adaptive benefit of episodic simulation and memory lies in guiding planning and prediction. The novel hypothesis proposed here is that episodic simulation and memory can also be harnessed to enhance empathy and, in turn, prosocial behavior. Thus, this work posits a previously unconsidered function of episodic simulation and memory: fostering empathy and prosocial behavior.

In sum, the landscape of research on memory is shifting of late with an emerging literature on memory's contribution to episodic simulation beginning to take shape. Researchers have already made substantial empirical headway, yet the precise cognitive and neural processes that guide simulation require further investigation. Moreover, although the importance of episodic simulation in shaping our everyday lives is continuing to elicit increased attention from researchers, almost no attention has been paid to a potential role of episodic simulation in supporting and enhancing the unique prosocial tendencies of our species. In three papers, this dissertation aims to further illuminate the cognitive processes that underlie episodic simulation and the functions it serves. Paper 1 characterizes age-related changes in remembering the past, imagining the future, and describing the present. Paper 2 delineates intrinsically related component cognitive and neural processes that contribute to imagining novel events. Paper 3 explores the role of imagining and remembering in facilitating prosocial intentions to help people in need.

Paper 1

Gaesser, B., Sacchetti, D. C., Addis, D. R., & Schacter, D. L. (2011). Characterizing age-related changes in remembering the past and imagining the future. *Psychology and Aging, 26*, 80-84.

Abstract

When remembering past events or imagining possible future events, older adults generate fewer episodic details than do younger adults. These results support the constructive episodic simulation hypothesis: deficits in retrieving episodic details underlie changes during memory and imagination. To examine the extent of this age-related reduction in specificity, we compared performance on memory and imagination tasks to a picture description task that does not require episodic memory. In two experiments, older adults exhibited comparable specificity reductions across all conditions. These findings emphasize the need to consider age-related changes in imagination and memory in a broader theoretical context.

Characterizing age-related changes in remembering the past and imagining the future

During the past several years, converging evidence from cognitive psychology, neuropsychology, and neuroimaging has documented that episodic memory – a neurocognitive system that supports recollection of personal experiences (Tulving, 2002) – also plays an important role in imagining or simulating future experiences (for recent reviews, see Schacter et al., 2008; Suddendorf & Corballis, 2007; Szpunar, 2010). Addis et al. (2008) extended this line of research to cognitive aging. Addis et al. (2008) used an adapted version of the Autobiographical Interview, a protocol developed by Levine et al. (2002) that segments individuals' descriptions of experiences into episodic or "internal" details (e.g., who, what, when, and where details) and "external" details (e.g., semantic information, other external events, repetitions). Levine et al. (2002) found that older adults produced fewer internal and more external details than did younger adults when recalling past autobiographical events.

In the Addis et al. (2008) experiment, older adults remembered past experiences or imagined future events in response to word cues, providing as much detail as possible for three minutes per episode. Replicating Levine et al. (2002), older adults provided fewer internal (episodic) details and more external (semantic) details than did younger adults when remembering the past. Importantly, Addis et al. (2008) documented a parallel aging deficit for imagining future events: older adults provided fewer internal details and more external details than did younger adults (see also, Addis, et al., 2010). Addis et al. (2008) interpreted these results as support for the *constructive episodic simulation hypothesis* (Schacter & Addis, 2007), which maintains that both remembering the past and imagining the future are supported by a constructive episodic memory system that is capable of flexibly recombining elements of prior experiences into simulations of future events. However, because the Autobiographical Interview

involves producing an extended narrative, differences between young and old adults in memory and imagination on the Autobiographical Interview could also reflect age deficits in non-episodic mechanisms.

To address this issue, we report two experiments that include a condition absent from previous studies using the Autobiographical Interview. Older and younger adults were instructed to describe a complex picture of a natural scene in as much detail as possible. The key question is whether the pattern previously observed for memory and imagination –reduced internal and increased external for older adults relative to young- also extends to a picture description task that does not require episodic memory.

Experiment 1

Experiment 1 examines imagination for personal events relative to description of events presented in a picture - a condition in which access to episodic memory is not required for task performance.

Method

Participants

Sixteen healthy younger adults (age, 18-35 years, $M = 24.00$ years, 8 female) and sixteen older adults (age, 65-88 years $M = 74.21$ years, 10 female) with no history of neurological impairments participated in this study. All subjects had normal or corrected to normal vision. Older adults also performed normally on the Mini-Mental State Examination ($M = 28.75$, $SD = 1.44$). Older adults had on average completed more years of education than had younger adults, but the difference did not attain statistical significance (Older: $M=16.25$ years, $SD=3.38$; Younger: $M=14.56$, $SD=1.89$; $p=.09$).

Stimuli and Design

The study stimuli consisted of 12 colored photographs that depicted people engaged in a particular activity or set of activities. Successful generation of events was encouraged by selecting activities that both age groups could relate to; for example, lounging on a beach, enjoying a picnic in a park, or dance reception. For the duration of each trial, a picture (size, 964 x 734 pixels) was displayed on a computer with the relevant task instructions (Describe or Imagine). Trials were blocked by condition to reduce cognitive load and facilitate older adults' comprehension of instructions. Presentation order of conditions was counterbalanced across subjects. Each condition included 2 practice trials and 4 experimental trials, consistent with our previous work with older adults using the Autobiographical Interview (Addis et al., 2008, 2010).

Autobiographical Interview

For each trial, participants completed an adapted version of Autobiographical Interview: they either described details about a picture or imagined an event using the picture as the general setting. General prompts were given when necessary to clarify instructions or solicit further details. For description trials, participants were required to describe the different people, objects, and environment in the picture and their relationship to one another (e.g. What are the people doing? What do they look like? Where are they?). Participants were instructed to report only what was literally depicted in the picture without embellishing. For imagination trials, participants imagined events that could possibly occur in the next few years with the picture as the general setting. Imagined experiences did not need to strictly involve the elements presented in the picture, so that participants would successfully generate an event. Events were restricted to the future few years, because the advanced age of some older adults meant they could not generate events far into the future. Participants were instructed to experience events from a field

perspective (through their own eyes) rather than from an observer perspective (from an external vantage point). Events generated for imagination trials were required to be specific in time and place, lasting several minutes to hours, but not exceeding a day. In all tasks, participants recounted as many details as possible for 3 minutes per picture.

Scoring

Consistent with previous studies of memory and imagination, we adapted the conventional Autobiographical Interview protocol developed by Levine et al. (2002) to systematically parse details in all tasks. Coders were assessed for interrater reliability on the basis of an intraclass correlation analysis for scores of 20 responses collected from previous studies, two-way mixed model; standardized Cronbach's $\alpha = .92$ for internal Autobiographical Interview scores and .85 for external scores). Importantly, the principal coder was blind to the hypotheses of this study so as to avoid a potential confirmation bias. For imagination trials, the central event was identified; if more than one event was mentioned, the event discussed in more detail was designated the central event. For the description trials, any perceptual detail that depicted elements in the picture as it was presented was considered part of the central event. Then the transcription was segmented into distinct details (e.g. unique chunks of information), and these details were categorized as internal (episodic detail relevant to the central event) or external (semantic details, repetitions, and irrelevant episodic details). While verbatim descriptions of items taken directly from the picture were scored as internal details for description trials, they were scored as external details for imagination trials, so that only actually imagined events counted toward internal details on imagination trials. Inferences about the picture (e.g. speculating about the temperature, providing explanations for peoples' actions) were

scored as external details for description trials. Coders referenced the appropriate pictures to classify details internal or external.

Results

We assessed age-related differences in picture description and imagination by conducting a mixed factorial 2 (Age: Young, Old) x 2 (Task: Describe, Imagine) x 2 (Detail: Internal, External) ANOVA. We found a significant main effect of Age, with older adults producing overall fewer details than did younger adults, $F(1,30) = 17.31, p < .01, \eta^2 = .36$, as well as a significant main effect for detail, indicating more internal than external details were provided across age and task $F(1,30) = 130.47, p < .01, \eta^2 = .81$. There was significant main effect of Task, reflecting more detail generated in the picture description condition than the imagination condition, $F(1,30) = 34.82, p < .01, \eta^2 = .537$. These main effects were qualified by a significant Age x Detail interaction: older adults generated fewer internal details and more external details, $F(1,30) = 24.48, p < .01, \eta^2 = .45$, compared with young adults (Figure 1.1A). No Age x Task ($F(1,30) = .45, p = .51, \eta^2 = .015$) or Age x Task x Detail ($F(1,30) = .01, p = .97, \eta^2 = .00$) interactions were observed. The finding that older adults produced fewer internal details than did young adults indicated an age-related deficit in episodic specificity consistent with previous findings.

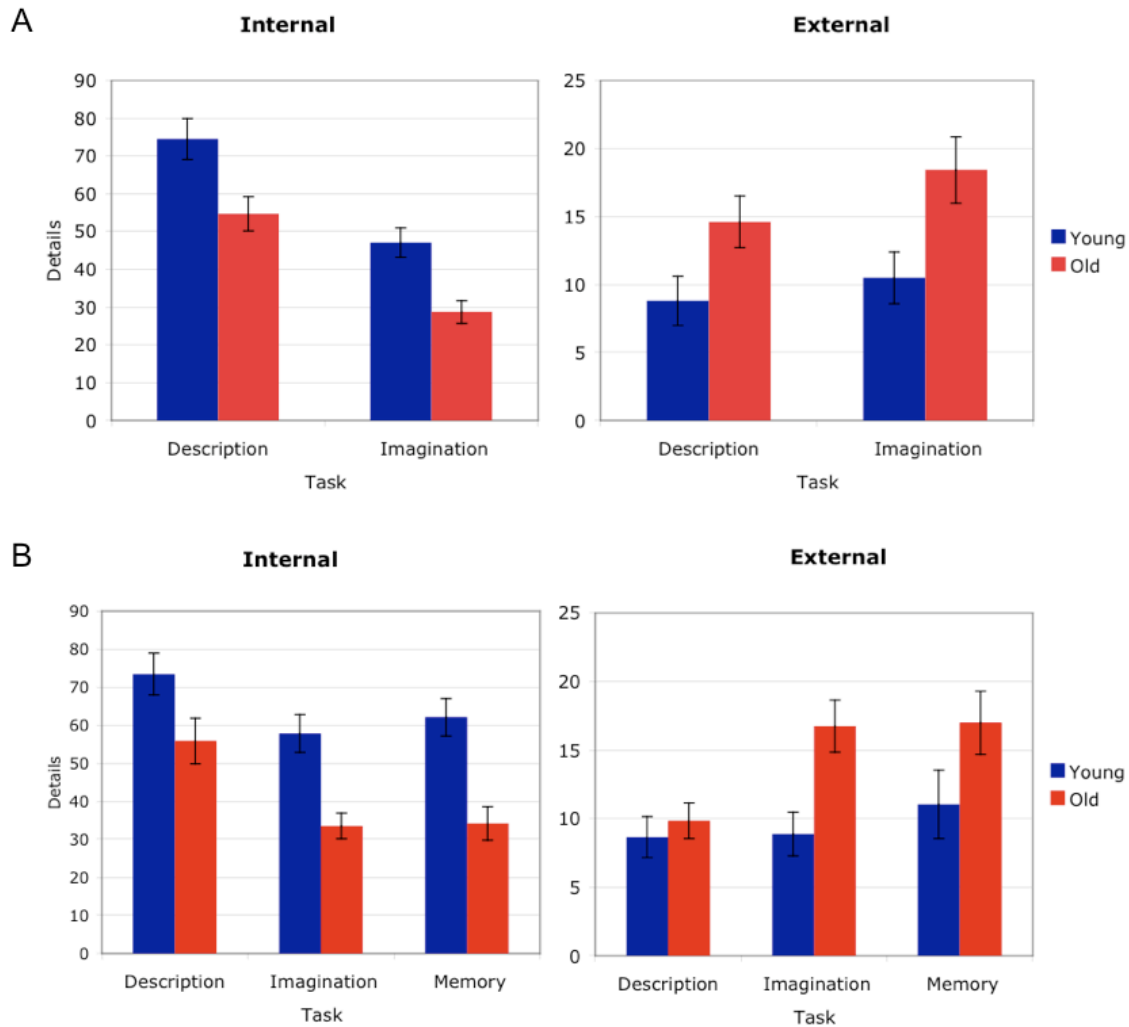


Figure 1.1 A) Mean number of internal and external details for Exp. 1 as a function of Age (Young, Old) and Task (Picture Description, Imagination). Error bars represent standard errors of the means. B) Mean number of internal and external details for Exp. 2 as a function of Age (Young, Old) and Task (Picture Description, Imagination, Memory). Error bars represent standard errors of the means.

To further evaluate the contribution of aging to reduced episodic specificity of imagination performance, we conducted a hierarchical multiple regression analysis with episodic (internal) detail of imagined events as the dependent variable and picture description performance (internal details) and age as predictors. After entering picture description performance into the model, age-related performance in the imagination condition was loaded. The analysis revealed that number of internal details provided in the picture description

condition was a significant predictor of number of internal details provided in the imagination condition, $R^2 = .455$, $F(1,30) = 25.01$, $p < .001$. When age was added in the second step, it predicted a significant but relatively small amount of variance in number of details provided in the imagination condition, R^2 change = .13, $F(1,30) = 9.09$, $p < .01$. The hierarchical multiple regression thus showed that, while relatively weak, there was an age-related deficit in imagination that could not be attributed to general descriptive ability.

Experiment 2

Experiment 1 yielded three key results. First, using pictorial cues in the imagination condition, we replicated previous findings in studies using word cues that older adults produce fewer internal and more external details than younger adults (Addis et al., 2008, 2010). Second, we extended this pattern to a picture description task that does not require episodic memory. Third, we found that while picture description performance was a significant predictor of imagination performance, age accounted for some variance in imagination performance, above and beyond picture description performance. In Experiment 2, we attempted to determine whether a) the key results from Experiment 1 could be replicated, and b) they extend to an autobiographical memory condition in addition to picture description and imagination conditions. Including an autobiographical memory condition should allow us to observe whether the small age-related deficit in imagination we found would remain after controlling for decline in episodic specificity of general descriptive ability *and* remembering personal experiences.

Method

Participants

Fifteen healthy younger adults (age, 19-35 years, $M = 25.00$ years, 5 female) and fifteen older adults (age, 65-88 years $M = 74.08$ years, 6 female) with no history of neurological

impairment participated in this study. All subjects had normal or corrected to normal vision. Older adults also performed normally on the Mini-Mental State Examination ($M = 28.93$, $SD = 3.21$). Older and younger adults completed a similar number of years of education, (Older: $M = 16.4$ years, $SD = 32.35$; Younger: $M = 15.47$, $SD = 1.85$; $p = .23$).

Stimuli, Design, Autobiographical Interview, and Scoring

Six color photographs were added to the stimuli used in Experiment 1, consisting of the same parameters as the original photographs. Procedures for Experiment 2 were the same as in Experiment 1, but with the addition of an autobiographical memory condition. Memory trials involved remembering a personal event that occurred in the last few years (versus the next few years for imagined events) using the picture as a cue to help focus on an event. Participants were instructed to remember events related to the contents of the picture, but events did not need to strictly consist of the exact situation depicted in the picture. Memories were required to be specific in time and place, lasting several minutes to hours, but not exceeding a day. Participants were instructed to experience events from a field perspective rather than from an observer perspective. Scoring for description and imagination trials was the same as in Experiment 1, and memory trials were scored according to Autobiographical Interview protocol in a similar manner to imagination trials from Experiment 1. As in Experiment 1, each condition included 2 practice trials and 4 experimental trials. Trials were blocked by condition, and presentation order of conditions was counterbalanced across subjects.

Results

We assessed age-related differences in picture description, memory, and imagination by conducting a mixed factorial 2 (Age: Young, Old) x 3 (Task: Describe, Remember, Imagine) 2 (Detail: Internal, External) ANOVA. Once again, we found significant main effects of Age

$F(1,28) = 8.44, p < .01, \eta^2 = .232$, and Detail, $F(1,28) = 124.78, p < .01, \eta^2 = .817$, qualified by an interaction: compared with younger adults, on the imagination, memory, and picture description tasks, older adults generated fewer internal details and more external details $F(1,28) = 15.01, p < .01, \eta^2 = .349$ (Figure 1.1B). There was also a significant main effect for Task, $F(1,28) = 26.05, p < .01, \eta^2 = .482$. Post hoc Bonferroni corrected pairwise t-test revealed that more details were generated for picture description than memory or imagination, $p < .025$. No Age x Task interaction ($F(1,28) = 1.04, p = .36, \eta^2 = .04$) or Age x Task x Detail interaction ($F(1,28) = 3.63, p = .07, \eta^2 = .16$) was found.

To assess the contribution of aging to imagination and memory performance beyond a general ability to describe events, we conducted two hierarchical multiple regression analyses; one with episodic (internal) detail in the imagination condition as the dependent variable and picture description performance (internal details) and age as predictors, the other with episodic (internal) details in the memory condition as the dependent variable and picture description performance (internal details) and age as predictors. Consistent with the first experiment, our analysis revealed that the number of internal details produced in the picture description condition was a significant predictor of internal details produced in the imagination condition, $R^2 = .737, F(1,28) = 78.343, p < .001$. When age was added in the second step, it significantly (though modestly) improved the model's capacity to account for variance in the imagination condition, $R^2 \text{ change} = .09, F(1,28) = 14.126, p < .001$. Similarly, for the second hierarchical regression model, number of internal details in the picture description condition was also a significant predictor of internal details in the memory condition, $R^2 = .783, F(1,28) = 44.317, p < .001$. When age was added as a predictor of internal details in the memory condition it significantly – but again only modestly- improved, $R^2 \text{ change} = .123, F(1,28) = 13.877, p < .001$. Of theoretical

interest is whether an aging imagination deficit remains above and beyond *both* a difference in descriptive ability *and* deficits in memory. To this end, we conducted a hierarchical regression entering description and then memory performance in separate blocks before adding age. As expected, the number of internal details in the picture description condition was a significant predictor of imagination performance ($R^2 = .783$, $F(1,28) = 78.343$, $p < .001$). Adding number of internal details in the memory condition as a predictor slightly but significantly improved the model (R^2 change = .076, $F(1,28) = 10.916$, $p < .01$). Interestingly, we found a small but significant imagination-specific deficit, R^2 change = .030, $F(1,28) = 4.915$, $p = .036$.

Discussion

The two experiments reported here provide novel information concerning the basis of age-related reductions in the specificity of remembered past events and imagined future events. If age-related deficits in episodic detail of imagining and remembering could be attributed entirely to impairments specific to memory function, we would have expected the age-related impairment in episodic detail for the picture description task to be reduced or non-existent relative to impairment evident for the imagination and memory tasks. Alternatively, if mechanisms other than memory contribute to performance on the memory or imagination tasks, we would expect parallel patterns across all tasks. While we replicated previous findings of age-related reductions in episodic specificity for remembered and imagined events (Addis et al., 2008, 2010; Levine et al., 2002), we also extended the pattern to picture description. Moreover, performance on the picture description task accounted for the bulk of variance in memory and imagination performance. Nonetheless, there was a significant albeit modest contribution of aging to memory and imagination performance above-and-beyond picture description performance.

Our findings have a number of implications for the constructive episodic simulation hypothesis (Schacter & Addis, 2007), which holds that age deficits in imagining future events reflect a problem in retrieving details from prior episodes and recombining them into a novel imaginary scenarios. The similar performance of older adults on picture description, imagination, and memory tasks appears to indicate that mechanisms other than episodic memory are also relevant to understanding previous observations of parallel age-related declines in episodic specificity during memory and imagination.

For example, changes in narrative style (e.g., Coupland & Coupland, 1995; James et al., 1998; Labouvie-Vief & Blanchard-Fields, 1982), such that older adults maintain different communicative goals from younger adults – emphasizing personal meaning rather than a precise reiteration of events – could contribute to decreased internal and increased external details in older adults across all three tasks. Alternatively, age-related differences in the ability to inhibit task-irrelevant thought (e.g., Arbuckle & Gold, 1993; Zacks & Hasher, 1994) might result in fewer internal details as well as more details that are coded as external (for discussion, see Schacter et al., 2011). It is interesting to note in this regard that despite the possibility that the picture description task may be somewhat more concrete and constrained than the memory and imagination tasks, and therefore potentially less prone to influence from task-irrelevant thoughts, the identical pattern of internal and external details was observed across tasks. In any case, because our results do not distinguish between the foregoing hypotheses, future research will be needed to characterize the non-episodic sources of age differences in tasks like those used here. We think that such research could benefit from adopting new approaches to characterizing narrative discourse in older versus younger adults, such as that recently illustrated in recent work by Trunk and Abrams (2009).

Nonetheless, both experiments revealed that not all age-related reductions in internal details during memory and imagination were accounted for by picture description performance. These findings are consistent with the constructive episodic simulation hypothesis and indicate that age-related changes in processes emphasized by that hypothesis, such as impaired retrieval and recombination of episodic detail, merit further investigation. The finding from Experiment 2 that a small age deficit in imagination was observed even after controlling for memory performance raises the intriguing possibility that there are age-related changes in processes specific to imagination, such as recombining episodic details (Addis et al., 2010; Addis & Schacter, 2008; Schacter & Addis, 2009).

Finally, our findings have implications for studies that have used the Autobiographical Interview to examine memory in various patient populations. (cf., Levine et al., 2002; Levine, Svoboda, Turner, Mandic, & Mackey, 2009; McKinnon, Black, Miller, Moscovitch, & Levine, 2006; Murphy, Troyer, Levine, & Moscovitch, 2008; Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009; Rudoy, Weintraub, & Paller, 2009). Such studies have typically attempted to distinguish episodic and semantic contributions to autobiographical memory based on Autobiographical Interview performance. However, our findings indicate that one cannot simply assume that Autobiographical Interview performance reflects specifically the operation of memory mechanisms (see also Rudoy et al. (2009) for discussion of some related issues). Future studies using the Autobiographical Interview will need to incorporate a condition such as the picture description task used here, in which narratives are collected that do not require episodic memory, in order to provide a broader characterization of between-group differences in Autobiographical Interview performance and potentially relevant higher-order cognitive processes.

Paper 2:

Gaesser, B., Spreng, R. N., McLelland, V. C., Addis, D. R., & Schacter, D. L. (in press).
Imagining the future: evidence for a hippocampal contribution to constructive processing.
Hippocampus, doi: 10.1002/hipo.22152.

Abstract

Imagining future events and remembering past events rely on a common core network, but several regions within this network – including the hippocampus – show increased activity for imagining future events compared to remembering past events. It remains unclear whether this hippocampal activity reflects processes related to the demands of constructing details retrieved across disparate episodic memories into coherent imaginary events, encoding these events into memory, novelty detection, or some combination of these processes. We manipulated the degree of constructive processing by comparing activity associated with the initial construction of an imagined scenario with the re-construction of an imagined scenario (imagine vs. re-imagine). After accounting for effects of novelty and subsequent memory, we found that a region in the hippocampus was preferentially activated for newly constructed imagined events compared with re-imagined events. Our results suggest that the hippocampus may support several distinct but related processes that are critical for imagining future events, and they also indicate that a particular region within posterior hippocampus may uniquely contribute to the construction of imagined future events.

Imagining the future:

Evidence for a hippocampal contribution to constructive processing.

The capacity to imagine possible future events supports humans' ability to plan and prepare for new experiences in an adaptive manner. Whether preparing for a job interview, hunting for a new apartment, or anticipating a first date, mentally projecting ourselves into novel situations and simulating the potential consequences of different actions can help guide future decision-making (Buckner & Carroll, 2007; Gilbert & Wilson, 2007; Schacter & Addis, 2007; Schacter, 2012; Schacter et al., 2012). Considerable evidence indicates that imagining future events and remembering past events rely on a common core network that includes the hippocampus in addition to other medial temporal, parietal, and prefrontal regions (for review, see Schacter et al., 2012). However, the role of the hippocampus in imagining future experiences has recently been the subject of debate.

Neuroimaging studies have consistently found evidence for hippocampal activation when people imagine future events (for review, see Addis & Schacter, 2012; Schacter et al., 2012). Indeed, several studies have shown that activity in the hippocampus is *greater* for imagining compared to remembering (e.g. Addis et al., 2007; Weiler et al., 2010; Addis et al., 2011). It has been suggested that such activity reflects more intensive constructive processing during imagining than remembering, that is, the hippocampus may play a role in recombining details gleaned from disparate episodic memories into a coherent novel scenario (Schacter & Addis, 2007). Evidence consistent with the idea that hippocampal activity is associated with a recombination process comes from studies that have observed greater hippocampal activity when the degree of constructive processing is increased by manipulating the probability that the event will occur (i.e. greater hippocampal activation for low than high probability future events; Weiler

et al., 2010), the amount of recombined detail (Addis & Schacter, 2008) or the specificity of an imagined episode (Addis et al., 2011).

However, other findings call into question the possibility that the hippocampus plays a role in recombining details during the construction of imagined events. For example, hippocampal activity in neuroimaging studies is not always greater for imagined than remembered events; comparable levels of activity have been observed in some studies and greater hippocampal activity for remembering than imagining in others (for review and discussion, see Addis & Schacter, 2012; Schacter et al., 2012). Moreover, recent neuroimaging evidence reveals a role for the hippocampus in the successful encoding of imagined future events into episodic memory (Martin et al., 2011), raising the possibility that evidence for greater hippocampal activation during imagining than remembering reflects encoding-related activity. Finally, several studies of amnesic patients with hippocampal damage show that such patients exhibit impaired abilities to imagine coherent scenes and future events (Hassabis, Kumaran, Vann, et al., 2007; Andelman et al., 2010; Race et al., 2011; Romero & Moscovitch, 2012; see also, Tulving, 1985; Klein et al., 2002,), but others find no such impairments (Maguire et al., 2010; Squire et al., 2010; Hurley et al., 2011, Cooper et al., 2011).

Addis and Schacter (2012) suggested that these discrepant findings could be reconciled if different regions within the hippocampus support separate component processes underlying imagining and remembering. This multicomponent account proposes that the hippocampus contributes to distinct but related processes that support imagining future events, including retrieving episodic details, recombining those details into coherent scenarios, and encoding the newly formed scenarios into episodic memory. From this perspective, hippocampal activation in neuroimaging studies of episodic simulation could potentially reflect the contributions of any of

the three component processes, depending on the extent to which experimental conditions draw on each component. In neuropsychological studies of patient populations, partial damage to the hippocampus may impair specific component processes while leaving others relatively intact, thereby giving rise to differential patterns of impairment. Although the multicomponent view cannot resolve all discrepancies in the literature, it seems clear that elucidating the precise contribution of the hippocampus to imagination and future thinking requires teasing apart these intertwined component processes in a rigorous and controlled manner.

To clarify the contributions of the hippocampus to imagining future events, we drew on experimental recombination (Addis, Pan, et al., 2009), subsequent memory (Wagner et al., 1998), and task switching paradigms (Duncan et al., 2012). Participants imagined novel future events constructed from person, place, and object details taken from their own autobiographical memories. Subjects imagined some future events for the first time in the scanner, and re-imagined other events that they previously imagined the day before. Events imagined for the first time should elicit a greater recombination demand than re-imagining events because they require the initial integration of disparate details into an event. However, events imagined for the first time are also more novel than re-imagined events, making it difficult to determine whether differential hippocampal activity for imagined compared with re-imagined events reflects differences in recombination demand or differences in event novelty (van Mulukom, Schacter, Corballis, & Addis, 2013). To control for novelty differences between imagine and re-imagine conditions, recombined person, place, and object detail sets were observed in a pre-exposure session the day before scanning in which subjects imagined future events for some of these detail sets, and judged the relative pleasantness of the details for others. Thus, the novelty of the event details was held constant across these two conditions by virtue of equivalent pre-exposure to the

detail sets, but the details were integrated into a coherent future event in the imagine condition and were not integrated into a coherent event in the pleasantness condition. In the scanner, trials involved either switching tasks using the same detail sets as the previous day or repeating the imagining task. Thus, subjects 1) imagined future events for the first time using detail sets for which they had previously judged pleasantness, 2) judged the pleasantness of person, place, and object details for the first time using some of the detail sets for which they had previously imagined an event, or 3) re-imagined events using the remaining detail sets that they had previously imagined the day before. After scanning, participants completed a cued-recall test, thus allowing us to hold constant encoding success for imagined and re-imagined events. If the involvement of the hippocampus in constructing imagined future episodes includes a recombination process, then we would predict greater hippocampal activity for imagined compared to re-imagined events after controlling for both encoding- and novelty-related processing.

Materials and Methods

Participants

Twenty-four, right-handed healthy adults (16 females; age $M = 21.4$, $SD = 2.9$) with no prior history of psychiatric, neurological, or other medical impairment that could compromise cognitive function, and possessing normal or corrected-to-normal vision participated in this study. An additional nine participants were run but excluded from data analysis due to failure to produce enough successfully encoded trials (> 10 per successfully remembered condition), task noncompliance, or excessive movement. All participants provided written informed consent and were compensated for their participation according to ethical guidelines approved by the Harvard University Institutional Review Board.

Materials and procedure

Design. Subjects performed three main tasks of interest while in the scanner. They imagined future events for the first time using detail sets for which they had previously judged the relative pleasantness of details (*Imagine* condition), judged the relative pleasantness of details for the first time using some of the detail sets for which they had previously imagined an event (*Pleasant* condition), or re-imagined events using the remaining detail sets that they had previously imagined the day before (*Re-imagine* condition). Critically, both the *Imagine* and *Re-imagine* conditions consisted of detail sets that were retrieved from disparate episodic memories, but in the *Imagine* condition the details had previously been encountered during the pleasantness task, which did not require combining the details into a coherent episodic scenario, whereas in the *Re-imagine* condition, subjects had previously combined the details into a coherent episodic scenario. All conditions are matched for prior exposure to the person-location-object triplets.

Pre-scan: Autobiographical memory collection. Approximately one week ($M = 10.29$, $SD = 3.01$) prior to scanning, participants came into the laboratory and recalled 200 autobiographical memories from the past 15 years, writing a description for every memory. Participants were allowed access to Facebook and were provided with a sample list of common life events to facilitate retrieval of the required number of memories. Each memory had to be specific in time and place (i.e. episodic) and comprised of a unique person, location, and object that could not be duplicated across events. The experimenter checked on the participant about once every hour to review the participant's progress and to ensure that the reported memories complied with instructions. Any reported memories that failed to comply with instructions were not used as stimuli in subsequent sessions. Before returning for the next session, person, location,

and object details were recombined across memories, thereby creating 180 newly formed person-location-object sets that were derived from three separate autobiographical memories.

Pre-scan: Pre-exposure. The day prior to scanning, participants imagined future events involving 120 of these detail sets, and judged the relative pleasantness of the details for the remaining 60 sets. For the 120 imagined future event trials, participants silently imagined a specific novel event integrating the three details within a person-location-object set that could plausibly occur in next five years. For the 60 pleasantness trials, participants constructed a sentence ranking the relative pleasantness of details within a person-location-object set, “Wedding ring is more pleasant than JFK Park is more pleasant than Sally”, for example. Subjects were given 9 s to imagine an event or rank the pleasantness of details. Following these tasks, participants provided a unique title that briefly summarized a generated event or judgment (e.g. “Playing badminton with Adrian” for an imagined trial, “Wedding ring > JFK Park > Sally” for a pleasantness trial).

Scanning. Immediately before entering the scanner, participants were administered practice trials (one trial for each condition) and the experimenter ensured that all instructions were understood. In the scanner, trials consisted of either switching task conditions (judging the relative pleasantness of person-location-object details that were used to imagine future events during the pre-exposure session or vice versa) or repeating the imagining task using the same person-location-object detail sets as in the pre-exposure session (see Figure 2.1). For 9 s, task instruction prompts were presented along with person-location-object detail sets and event or judgment titles that participants generated the previous day. Presenting titles during scanning that summarize previously generated events or judgments holds constant differences that might reflect repeating or recalling experiences from the pre-exposure session; varying across

conditions is whether or not disparate details have been recombined into a specific imagined episode.

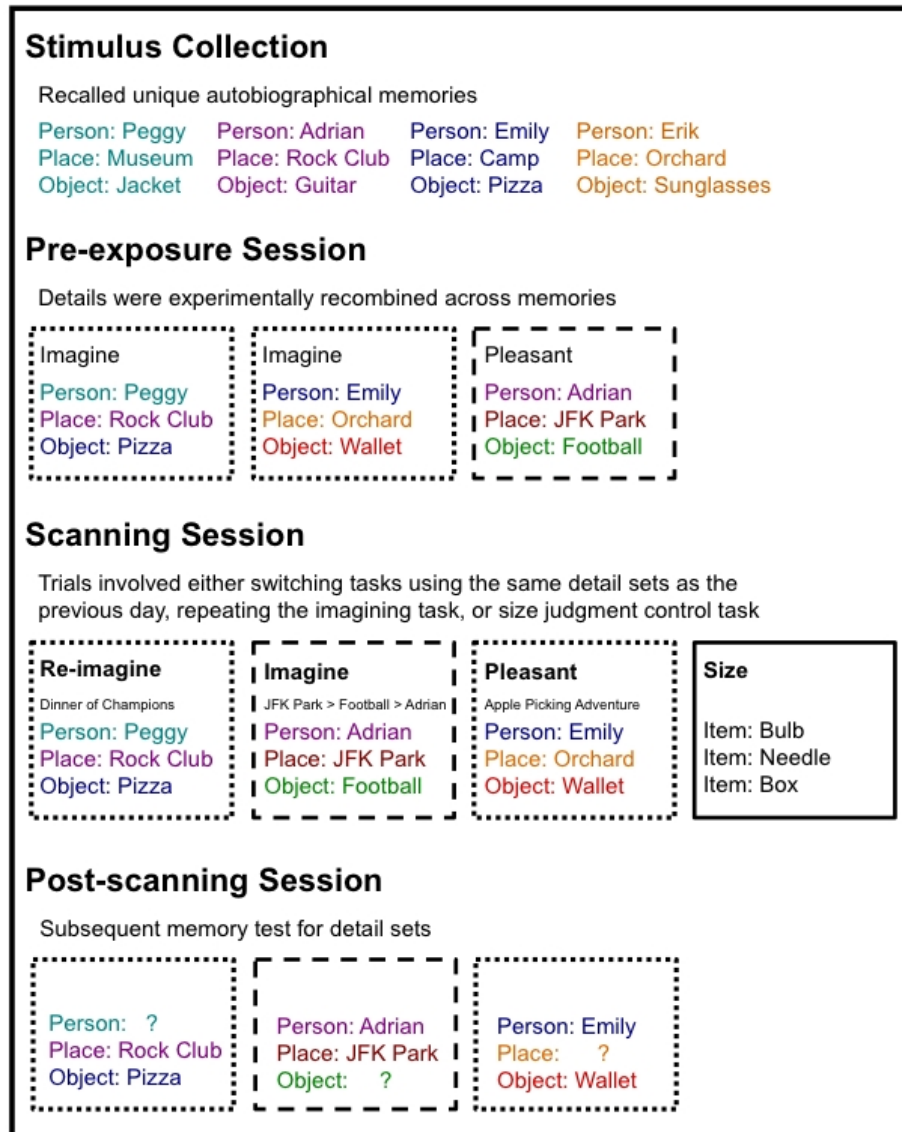


Figure 2.1. This study involved four experimental sessions. First, participants recalled autobiographical memories. Second, participants imagined events or made pleasantness judgments on detail-sets experimentally recombined across autobiographical memories. Third, participants re-imagined the same event from the previous session, imagined an event for the first time, made pleasantness for the first time, or completed a size judgment control task. Finally, subsequent memory performance was assessed with cued-recall test.

The experimental design yielded these three condition types (*Imagine*, *Pleasant*, *Re-imagine*) composed of 60 trials each labeled according to the task completed during scanning. Participants also completed 30 trials of size judgment task (*Size* condition) based on a previous study by Addis, Pan, et al. (2009), during which they had 9 s to integrate three nouns into a sentence that ranked the relative size of each item in a “X is bigger than Y is bigger than Z” format. Phenomenological ratings of how detailed the imagined event was (for *Imagine* and *Re-imagine* trials) or how difficult it was to make a relative judgment (for *Pleasantness* and *Size* trials) were collected using a button box (1 = low, 4 = high) for 3 s following imagining an event or making a relative judgment. These phenomenological ratings (i.e. detail and difficulty) not only offer information concerning subjective experiences, but also serve as an online indicator of task compliance in the scanner on a trial-by-trial basis, hence subsequent analyses only include trials during which participants provided a response. Notably, participants provided a response for 95% of trials, indicating a high rate of task compliance. Each trial (experimental task + phenomenological rating: 12 s) was randomly interleaved with 3, 6, or 9 s of fixation, allowing for an event-related analysis by establishing temporal jitter in the experimental design.

Post-scanning: Subsequent memory test. Ten minutes after the last experimental trial, participants completed a surprise cued-recall task using a procedure similar to that used in previous studies for testing memory of events with several elements (Jones, 1976; Martin et al., 2011; Szpunar, Addis, & Schacter, 2012). The test was composed of 180 trials, 60 trials each from the *Re-imagine*, *Imagine*, and *Pleasant* tasks presented during scanning. On every trial of the memory test, two of three details (person and place, place and object, or person and object) from a scanning trial were presented and the missing detail was to be recalled. Since participants were instructed during scanning to integrate all three details –either into a coherent event

(Imagine and Re-imagine), or by making a relative judgment (Pleasant) – subsequent memory for these details reflects how well these details were bound together. The detail to be recalled was counterbalanced across detail type (person, location, or object). Participants were instructed that they could guess if they felt reasonably certain of the right answer. The test was self-paced, lasting about one hour.

fMRI parameters and preprocessing. Brain imaging data were collected on a 3T Siemens Magnetom Tim Trio MRI scanner with a 12-channel phased-array whole-head coil. Anatomical scans were acquired using a T1-weighted high-resolution three-dimensional magnetization-prepared rapid gradient echo sequence (MPRAGE: 176 sagittal slices, TR = 2530 ms, TE = 1.64 ms, 7° flip angle, 1 mm isotropic voxels).

Six task blood-oxygen-level-dependent (BOLD) functional scans were acquired using a T2*-weighted echo-planar imaging (EPI) pulse sequence (47 interleaved axial slices parallel to the anterior-posterior commissure plane, TR = 3000 ms, TE = 30 ms, 85° flip angle, no skip between slices, 3 mm isotropic voxels). Task stimuli were presented using E-Prime software to display text that was projected onto a screen at the head of the scanner and reflected into a mirror on top of the head coil for the participant to see. Two additional 6 min 12 s resting state BOLD scans (not presented here) were acquired at the beginning and end of the scanning session. Cushions were used to minimize head movement during scanning. Participants made responses using a button box placed in their right hand.

Functional scans were preprocessed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK). To allow for T₁-saturation effects, the initial 4 volumes in each run were excluded from analyses. Data were corrected for slice-dependent timing differences and for head movement within and across runs using a rigid body correction. Data were then spatially

normalized to the standard space of the Montreal Neurological Institute (MNI) atlas (resampled at 2 mm cubic voxels), and spatially smoothed with a 6 mm full-width half-maximum Gaussian kernel. All coordinates are reported in MNI space.

After preprocessing, data were analyzed with the general linear model using SPM8. The BOLD responses for seven trial types (i.e. imagine hit, imagine miss, re-imagine hit, re-imagine miss, pleasant hit, pleasant miss, size sentence) were modeled for each participant. The onsets of these trials were then convolved with the canonical hemodynamic response function to create regressors of interest. In doing so we restricted our analyses to the neural activity related to the construction phase of simulating events and thereby minimize contamination by other cognitive processes including elaboration-related activity, consistent with previous methods (Addis et al., 2007; Martin et al. 2011). Additional covariates of no interest (a session mean, a linear trend, and subject-specific movement parameters) were also modeled. First-level planned contrasts (i.e. fixed effects models) were performed on these parameter estimates, and contrast images for each participant were subsequently entered into a second-level analysis treating participants as random effects. For the imagine and re-imagine conditions, linear parametric modulation regressors of detail ratings were included to (1) ensure that differences between conditions are not simply attributed to the amount of details retrieved and (2) account for known detail modulation effects in the hippocampus (Addis & Schacter, 2008; Martin et al., 2011).

Contrasts of interest were run in order to identify regions preferentially engaged by: (1) **imagining future events** by comparing imagined future events relative to the semantic control task (i.e. $Re-imagine + Imagine > Size$); and (2) **constructing novel future events** by comparing initial simulations with repeated simulations (i.e. $Imagine > Re-imagine$). The two analyses were confined to successfully remembered trials, allowing us to hold constant encoding-related

activity (i.e. *Imagine* > *Re-imagine*, for hits only). However, as noted in the Introduction, a simple comparison of Imagine and Re-imagine conditions does not allow us to distinguish constructive activity or recombination demand on the one hand, and event novelty on the other. To remove activity related to task novelty, we performed an additional analysis in which we subtracted activity from the *Pleasant* condition (i.e. [*Imagine* > *Pleasant*] > [*Re-imagine* > *Pleasant*]). As noted earlier, this condition controls for novelty because, just like in the Re-imagine condition, it elicits activity related to the retrieval of disparate details across episodic memories, but unlike in the Re-imagine condition, the relative pleasantness of these details must be judged for the first time. Thus, we computed the following contrast to control for activity related to both encoding and novelty (i.e. [*Imagine* > *Pleasant*] > [*Re-imagine* > *Pleasant*], for hits only).

The minimum cluster size required for corrected significance was calculated using the 3dClustSim (an adaptation of AlphaSim) AFNI program, which estimates the overall probability of false positives within a search volume through a Monte Carlo simulation (10,000 iterations). For whole-brain contrasts, we report all activations at a voxel-level threshold of $p = .001$ combined with a spatial extent threshold of 89 voxels, yielding a threshold of $p < .05$ corrected for multiple comparisons. Since the hippocampus was an a priori region of interest, we calculated a corrected threshold using a bilateral hippocampal volume (1,878 2mm^3 voxels), setting a $p < .05$ threshold with a $p = .005$ voxel-level threshold and extent threshold of 17 voxels (Yassa & Stark, 2008).

Results

Behavioral Results

Behavioral data confirmed participant compliance during scanning as well as in the post-scan session. Comparisons were performed using a paired-samples t-test or repeated measures ANOVA (Bonferroni correction for multiple comparisons, $\alpha < .05$), where appropriate. On a 4-point Likert scale (1 = low detail, 4 = high detail), re-imagined future events were rated significantly more detailed ($M = 2.87$, $SE = 0.10$) than imagined future events ($M = 2.73$, $SE = .10$), $t(23) = 2.58$, $p = .017$ (see Table 2.1). In addition to ratings serving as an indicator of subject compliance on a trial-by-trial basis during scanning, this pattern of detail ratings suggests that during the pre-exposure session, participants were able to comply with task instructions to either discretely imagine an event, or to judge the pleasantness of details without constructing an imagined event during the Pre-exposure phase: if subjects had imagined events during the pleasantness task, one would expect detail ratings to be similar across Imagine and Re-imagine conditions, but this was not the case. Subsequently-remembered imagined and re-imagined events (hits) were significantly more detailed ($M = 3.01$, $SE = .08$) than subsequently forgotten imagined and re-imagined events (misses; $M = 2.59$, $SE = .10$), $t(23) = 7.88$, $p < .001$. Although detail ratings significantly differed across Imagine and Re-imagine conditions and predicted subsequent memory performance, since detail ratings were included in SPM as parametric modulator, any changes in BOLD signal associated with detail would be accounted for in our model.

Table 2.1

Behavioral results

Subsequent Memory	Imagine	Re-imagine	Pleasant
	Mean detail rating (and SE)		
Hit	2.94 (.08)	3.08 (.08)	
Miss	2.51 (.01)	2.66 (.09)	
Hit and Miss	2.73 (.01)	2.87 (.01)	
		Mean # of trials (and SE)	
Hit	27.45 (2.37)	44.71 (1.51)	22.45 (1.62)
Miss	28.83 (2.23)	12.17 (1.35)	35.17 (1.79)
Hit and Miss	56.29 (1.08)	56.89 (0.81)	57.63 (1.13)

To evaluate subsequent memory differences across experimental tasks, we compared difference scores (subtracting the number of misses from the number of hits) for each experimental task. The difference scores were as follows: Re-imagine ($M = 32.54$, $SE = 2.74$), Imagine ($M = -1.38$, $SE = 4.48$), Pleasantness ($M = -12.70$, $SE = 3.21$). The number of hits compared to misses systematically varied across conditions ($F(2,46) = 95.20$, $p < .001$). Re-imagine trials were more likely to be subsequently remembered than Imagine and Pleasant trials. Further, Imagine trials were more likely to be remembered than Pleasant trials. Although one must be cautious interpreting subsequent memory effects (i.e. hits compared to misses) from different bin sizes across conditions to avoid confounding effects of experimental task with

subsequent memory, these observed differences should not systematically bias interpreting differences in BOLD signal across conditions restricted to subsequently remembered items only.

fMRI Results

Imagining future events. Imagination conditions, relative to the semantic control task (i.e. Imagine + Re-imagine > Size), revealed activation in medial prefrontal cortex, posterior cingulate cortex, retrosplenial cortex, middle frontal gyrus, lateral and medial temporal lobes, consistent with many previous studies (for review, Schacter et al., 2012) (see Table 2.2 Figure 2.2A).

Table 2.2

FMRI results: whole-brain

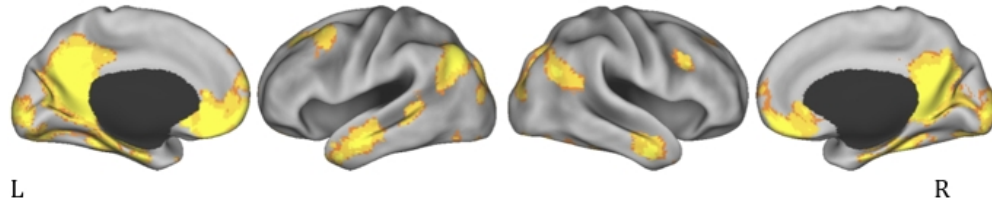
Brain Region	peak MNI coordinate (x, y, z)	Z-score
<i>Re-imagine + Imagine > Size Control</i>		
R Posterior Cingulate	2, -56, 22	7.32
L Ventral MPFC	-8, 36, -14	6.66
L Middle Temporal Gyrus	-58, -6, -18	6.57
R Middle Temporal Gyrus	52, -6, -26	5.67
R Precuneus	6, -56, 50	5.44
L Superior Frontal Gyrus	-20, 30, 46	5.33
L Superior Frontal Gyrus	-12, 54, 46	5.02
R Temporal Pole	40, 20, -38	4.82
R Middle Frontal Gyrus	42, 14, 30	4.75
R Cerebellum	14, -72, -30	4.23
R Cerebellum	14, -88, -40	4.16
R Orbital Frontal cortex	30, 26, -24	3.99
R Superior frontal gyrus	24, 26, 44	3.68
<i>Imagine > Re-imagine</i>		
L Lateral occipital gyrus	-26, -88, 18	5.50
R Anterior Precuneus	-6, -54, 50	4.89
R Fusiform Gyrus	24, -84, -6	4.72
R Fusiform Gyrus	30, -84, -6	4.72
R Superior Frontal Gyrus	32, 20, 62	4.52
Table 2.2 (continued)		

Table 2.2 (Continued)

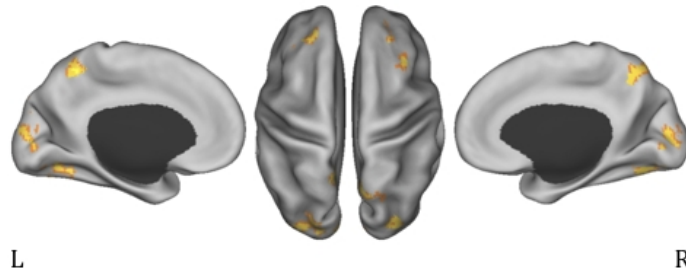
L Superior Frontal Gyrus	-26, 40, 42	4.42
L Inferior Temporal Gyrus	-38, -58, -4	4.33
<i>(Imagine > Pleasant) > (Re-imagine > Pleasant) hits only</i>		
R Superior Frontal Gyrus	24, 22, 56	4.77
L Lateral Occipital Gyrus	-24, -88, 20	4.67
R Superior Parietal Lobule	20, -70, 56	4.64
L Fusiform Gyrus	-26, -84, -4	4.38
Calcarine Cortex	0, -90, 4	4.36
L Superior Parietal Lobule	-20, -62, 52	3.97
<i>Re-imagine > Imagine, hits only</i>		
L Inferior Frontal Gyrus	-42, 28, -8	4.74
L Middle Temporal Gyrus	-48, -28, -10	4.27
L Angular Gyrus	-40, -60, 44	4.20
L Posterior Precuneus	-8, -70, 34	4.05

Note. All activations are significant at a $p < .05$ threshold corrected for multiple comparisons with a $p = .001$ voxel-level threshold and extent threshold of 89 voxels. MNI, Montreal Neurological Institute; L, left; R, right.

A. (Imagine + Re-imagine > Size)



B. (Imagine > Re-imagine)



C. (Imagine > Pleasant > Re-imagine > Pleasant) hits only

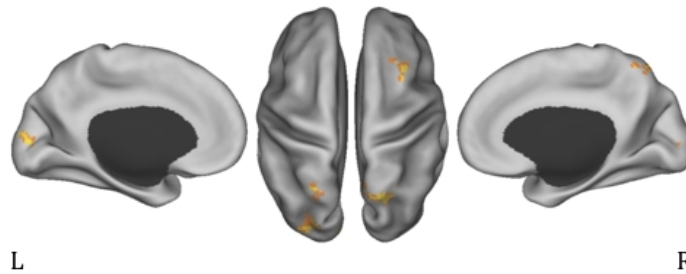


Figure 2.2. Whole-brain activations are significant at a $P < 0.05$ threshold corrected for multiple comparisons with a $P = 0.001$ voxel-level threshold and minimum extent threshold of 89 voxels. L, left; R, right.

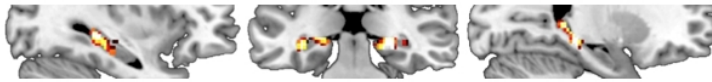
Encoding and novelty in the hippocampus. To examine novelty processing, we contrasted conditions that involved switching tasks across sessions to the condition that repeats the same task (Pleasant 1 Imagine > Re-Imagine). This contrast showed significant activity in regions (222, 226, 28; 22, 228, 26) near the midline of the long axis of hippocampus extending anteriorly, similar to previous observations (e.g. Kumaran & Maguire, 2007). To examine encoding effects, we contrasted hits versus misses collapsed across Imagine and Re-imagine

conditions. Consistent with Martin et al. (2011), we observed evidence that the anterior hippocampus supports encoding activity. Our analysis revealed a single cluster (228, 26, 228) activated at a voxelwise threshold of $P \leq 0.012$ which when combined with a spatial extent of 21 voxels in 3dClustSim approached a corrected threshold of $P \leq 0.10$. While this hippocampal activity is only suggestive, most likely because we had far fewer trials than did Martin et al. (2011) due to design constraints of our study, the activity observed here generally aligns well with the findings of Martin et al. (2011).

Constructing future events: hippocampal analysis. Contrasting activation engaged by imagining an event for the first time compared to re-imagining the same event (*Imagine > Re-imagine*) elicited greater activity in the right anterior and bilateral posterior hippocampus. This contrast revealed candidate regions that could support a constructive process, since imagining an event for the first time requires the initial construction of disparate details into an event rather than the less intensive processing of re-construction. However, as pointed out earlier, this contrast does not allow us to separate processes associated with construction of imagined events from those associated with novelty detection or encoding. To control for these confounds, we ran a tighter contrast that removed activity associated with novelty of event details (*Pleasant condition*) and held encoding constant by constraining our analysis to hits only (i.e. [*Imagine > Pleasant*] > [*Re-imagine > Pleasant*], for hits only). This more rigorous contrast revealed that only the left posterior hippocampus remained preferentially engaged (see Figure 2.3, Table 2.3).

A. (Imagine > Re-imagine)

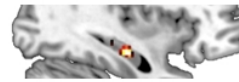
Posterior



L

R

Anterior



R

B. (Imagine > Pleasant > Re-imagine > Pleasant) hits only

Posterior



L

Figure 2.3. As the hippocampus was an a priori region of interest, activations are presented at a $P < 0.05$ threshold corrected for multiple comparisons with a $P=0.005$ voxel-level threshold and extent threshold of 17 voxels with the whole brain masked to only show voxels within the bilateral hippocampus. L, left; R, right.

Table 2.3

FMRI results: hippocampal masked

Brain Region	peak MNI coordinate (x, y, z)	Z-score
<i>Imagine > Re-imagine</i>		
Anterior Right Hippocampus	36, -18, -14	3.25
Posterior Right Hippocampus	24, -28, -10	3.69
Posterior Left Hippocampus	-36, -34, -6	3.69
<i>(Imagine > Pleasant) > (Re-imagine > Pleasant) hits only</i>		
Posterior Left Hippocampus	-36, -36, -6	3.22

Note. Activations are significant at a $p < .05$ threshold corrected for multiple comparisons with a $p = .005$ voxel-level threshold and extent threshold of 17 voxels. MNI, Montreal Neurological Institute; L, left; R, right.

Constructing future events: whole brain analysis. Contrasting activation during imagining an event for the first time compared to re-imagining the same event (*Imagine > Re-imagine*) revealed increased activity in the superior frontal gyri and regions in occipital and temporal cortex related to visual/imagery processing (see Table 2.2, Figure 2.2B). We then controlled for novelty- and encoding-related activity by subtracting activity associated with the Pleasant condition and held subsequent memory performance constant (i.e. [*Imagine > Pleasant*] > [*Re-imagine > Pleasant*], *for hits only*) This contrast showed activity in bilateral parietal lobes as well as activity in regions related to visual/imagery processing, but now most prominently observed was activity in the right superior frontal gyrus (see Table 2.2, Figure 2.2C). We also examined increases in activity for repeated simulations (*Re-imagine > Imagine*). This contrast revealed greater activity for re-imagining compared to imagining in the superior precuneus, inferior frontal gyrus, and lateral temporal cortex (see Table 2.2).

Discussion

A distributed network of brain regions that includes the hippocampus is commonly activated for remembering the past and imagining the future (Buckner & Carroll, 2007; Hassabis & Maguire, 2007; Schacter et al., 2007; Spreng et al., 2009; Schacter et al., 2012). Moreover, the hippocampus has also shown increased activity for imagining compared to remembering (e.g. Addis et al., 2007; Weiler et al., 2010; Addis et al., 2011). It has been proposed that this preferential hippocampal activity reflects the increased recombination demand associated with integrating disparate episodic details into coherent scenarios (Schacter & Addis, 2007). The aim of the present study was to evaluate this hypothesis by examining whether hippocampal activity is sensitive to differences in constructive demand after controlling for both encoding- and novelty-related activity. Our findings suggest that the hippocampal contributions to imagining

future events extend beyond encoding and novelty processing because even with these processes controlled for, left posterior hippocampus was involved in the constructive process of recombining disparate details from memory into a coherent scenario when simulating a future event.

Although previous studies have observed increased hippocampal activity under conditions that have been interpreted as reflecting a more intensive or demanding constructive processing (Addis et al., 2007, 2011; Addis & Schacter, 2008; Weiler et al., 2010), the confounding influences of encoding- and novelty-related processes have made this claim difficult to evaluate. Our results thus provide some support to previous interpretations of increased hippocampal activation during imagining compared with remembering as reflecting differences in recombination processing (e.g. Addis et al, 2007). Although a few studies have found that remembering past events evokes greater activity than imagining future events (Hassabis, Kumaran, & Maguire, 2007; Botzung, Denkova, & Manning, 2008; D'Argembeau, Xue, Lu, Van der Linden, & Bechara, 2008), the paradigms used in these studies required subjects to pre-imagine events before being scanned, thereby reducing constructive demand during the scanning session. Thus, rather than offering contradictory findings, these studies suggest that the online construction of imagined events is an important feature to consider when interpreting existing results and designing future studies.

While the evidence for a constructive, recombinatory process in the hippocampus under the stringent conditions of the present experiment provides support for the idea that the hippocampus plays a role in generating imagined events, the anterior-posterior localization of this activity conflicts with previous reports that the anterior hippocampus in particular underlies recombination (Addis et al., 2007; Schacter & Addis, 2009; Weiler et al., 2010). One possible

explanation is that the anterior hippocampal activity in these studies reflects the encoding of novel episodes as opposed to their construction. Consistent with the anterior hippocampus reflecting the encoding of novel imagined events, Martin et al. (2011) showed that this region was more active for successfully remembered compared to successfully forgotten imagined future events constructed online in the scanner. They also observed a cluster in the posterior hippocampus that was greater for successfully remembered versus forgotten imagined events. However, in the absence of a manipulation that distinguishes encoding processes from recombination processes, it is difficult to tease apart a constructive process that requires the binding of details into a coherent event from processes that support the successful encoding of those details into an enduring memory trace.

Further evidence suggesting that the anterior hippocampus encodes novel episodes comes from a number of studies that demonstrate an encoding-retrieval distribution along the anterior-posterior axis of the hippocampus with the anterior supporting encoding and the posterior supporting retrieval (Lepage, Habib, & Tulving, 1998; Schacter & Wagner, 1999; Spaniol et al., 2009). Moreover, the anterior hippocampus appears particularly engaged when encoding associative information (Kirwan & Stark, 2004; Chua, Schacter, Rand-Giovannetti, & Sperling, 2007). However, we must be cautious about making strong claims exclusively linking the posterior hippocampus with recombination processes. For example, a recent meta-analysis of neuroimaging studies investigating medial temporal lobe activity during remembering and imagining tasks revealed that a number of parameters (i.e. type of cue, task, event specificity) can impact the precise location of activity in the hippocampus and related regions (Viard, Desgranges, Eustache, & Piolino, 2012). Future studies capable of distinguishing constructive

processing from encoding using a variety of such manipulations are needed before making strong claims.

Given the involvement of the posterior hippocampus in spatial processing (Maguire et al., 2000; Hassabis, Kumaran, Vann, et al., 2007), it may be that this region supports the formation of a coherent spatiotemporal representation from disparate episodic details. Indeed, to the extent that simulations of future events meaningfully inform planning and preparation, this process seems critical. If the idea has merit, amnesic patients with posterior hippocampal damage should exhibit problems forming a coherent spatiotemporal imagined event, but as noted earlier the nature and even existence of imagination deficits in hippocampal amnesics is currently the topic of intensive debate (cf., Maguire & Hassabis, 2011; Squire et al., 2010; for review, see Addis & Schacter, 2012). Although most reported cases of hippocampal amnesic patients exhibiting an intact ability to construct imagined events have not included measures of event integration or spatial coherence (e.g. Squire et al., 2010), Maguire and Hassabis (2011) claim that the patients studied by Squire et al. (2010) appear to exhibit a reduction in spatial details relative to typical numbers generated by controls.

Evidence potentially relevant to our findings comes from Hassabis et al. (2007), who found that four of five amnesic subjects showed imagination deficits on their scene construction task. Nonetheless, they did observe one amnesic patient with a spared ability to vividly imagine events, PO1. PO1 suffered from dense amnesia, with 50% bilateral hippocampal volume loss, and a preserved ability to construct imagined scenarios—including unimpaired performance on measures of spatial coherence. This patient displayed signs of intact hippocampal tissue, raising the possibility that preserved ability to construct novel scenarios is dependent on residual hippocampal tissue. Using fMRI to scan PO1, Mullally, Hassabis, and Maguire (2012) observed

two regions in the patient's medial temporal lobe that were more active for imagining coherent scenarios compared to imagining acontextual objects, the hippocampus (36, -28, -14) and the parahippocampus (33, -46, -5). Interestingly, the region we found to be associated with recombination in the present study is between these coordinates along the longitudinal axis. Of course, making inferences regarding the axis of the hippocampus across intact and severely atrophied hippocampi must be done with great caution, because the possibility of a potential functional reorganization induced by the lesion remains unknown.

The pattern of posterior hippocampus activity we observed in the present study also aligns nicely with ideas presented in a recent review of long-axis functional specialization in the hippocampus. In their review, Poppenk, Evensmoen, Moscovitch, and Nadel (2013) proposed that differences in network connectivity and subfield composition better position the posterior hippocampus to represent fine-grained information compared with the anterior hippocampus, which preferentially represents more global features. From this perspective, imagining an event for the first time may require the initial construction of precise spatial and temporal details, whereas re-imagining the same event does not elicit the same degree of fine-grained construction. Further research is needed to directly test how these local and global functional specializations contribute to representations of imagined future events.

One limitation of our study is that while we infer a difference in the degree of constructive processing between imagining an event for the first time and re-imagining the same event, we did not collect independent measures of constructive processing across these tasks. One way for future research to overcome this limitation would be to collect difficulty ratings for all conditions (we collected difficult ratings only for the Pleasant and Size conditions): more

demanding constructive processing should elicit greater difficulty ratings compared with less intensive constructive processing.

Differences observed between imagining and re-imagining could also be attributed to differences resulting from some form of priming (i.e., the imagine condition could be conceived as an unprimed condition whereas the re-imagine condition could be conceived as a primed condition). However, recent studies examining future event simulation using a repetition suppression paradigm (van Mulukom et al., 2013; Szpunar et al., in press), which measures effects similar to priming, did not report changes in posterior hippocampal activity, and therefore priming effects are unlikely to explain the difference between imagining and re-imagining observed here. However, these differences might be related to differences in encoding and/or retrieval. While we attempted to control encoding-related activity by matching subsequent memory performance of imagined details (i.e. person, place, or object sets), this procedure equates for encoding success; it is possible that imagining requires greater encoding effort than does re-imagining; conversely, re-imagining may require greater retrieval processing of the pre-exposure session than imagining does.

It is also worth noting that while the experimental design we used here controlled for the novelty of retrieving disparate episodic details (a requirement of both Imagine and Re-imagine), and task novelty (by contrasting Imagine and Re-imagine with the Pleasant condition), it does not rule out the possibility that our data reflect the influence of novelty-related processing attributable to imagining new events. Events constructed for the first time (Imagine) are novel compared to events constructed for the second time (Re-imagine). Thus, activity in the hippocampus that we interpret as reflecting constructive processing could also be attributable to event novelty. However, event novelty is an inherent property of event construction, so the two

may be difficult to separate. Future research is needed to determine whether and to what extent it is possible to tease apart the close relationship between event novelty and construction of imagined future events.

Our results provide evidence that the hippocampus contributes to a constructive or recombinatory process that supports the ability to imagine future events. In light of other evidence that the hippocampus contributes to both encoding and novelty detection processes, our findings are generally consistent with the multiple component view advanced by Addis and Schacter (2012), which holds that the hippocampus contributes to several distinct processes that support imagining future events, including recombining event details into coherent scenarios. Critical to the theoretical success of future studies will be mapping different subregions of the hippocampus to specific component processes using refined methods that allow for the closely related processes of retrieval, construction, and encoding to be differentiated. Employing high-resolution imaging may prove particularly useful to future progress as this method can reveal anatomy at the resolution of individual hippocampal subfields (Kerchner et al., 2010). As the hippocampus does not work in isolation, future studies should also develop approaches and theoretical models that directly evaluate how these component processes interact with the other processes embedded in the wider network supporting imagination.

Beyond the hippocampus, imagining and re-imagining events robustly recruited the distributed network associated with memory, future-thinking and related functions compared to our semantic control task (Buckner & Carroll, 2007; Schacter, et al., 2007; Spreng et al., 2009). The results from the current study draw particular attention to the role of the superior frontal gyrus (BA8) and the posterior precuneus. In regard to the activation of superior frontal gyrus for imagined relative to re-imagined events, there is converging evidence that right lateralized

activity in the superior and middle frontal gyrus is associated with inhibitory processes mediating controlled retrieval and encoding processes, such as suppressing the retrieval of unwanted learned associations (Anderson et al., 2004; Depue, Curran, & Banich, 2007; Wylie, Fox, & Taylor, 2008; Rizio & Dennis, 2013). This observation raises the intriguing – though speculative – possibility that the superior frontal gyrus may contribute to processes that actively isolate episodic details from their previous associations within autobiographical memories, perhaps transitively inhibiting the former associations from memory in order for details to be effectively recombined into a novel representation. In regard to the posterior precuneus, activity in this region increased with repeated imagining of an event rather than with event novelty; this pattern seems particularly robust because it has been observed across different paradigms that require repeated imagining of future events (van Mulukom et al., in press; Szpunar et al., in press). Exploring the precise role of regions beyond the hippocampus, including the superior frontal gyrus and the posterior precuneus, in imagining future constitutes an important task for future work.

It is only during the past few years that our understanding of the functional importance of the hippocampus has extended beyond the purview of remembering past experiences to include such functions as imagining future experiences or novel scenes (for reviews, see Buckner, 2010; Schacter & Addis, 2009; Schacter et al., 2012, Szpunar, 2010). As our investigation and understanding of imagining future events grows, the neural and cognitive processes shared by memory and imagination are beginning to come into view. But it also seems clear that processes that are preferentially recruited for imagining the future can potentially offer new theoretical insights into the functions of remembering the past, because a major adaptive function of episodic memory lies in its contribution to our ability to imagine novel events. In this way, we

are not strictly bound by past experiences, but instead can flexibly use past experiences to construct event simulations and plan for the future.

Paper 3:

Gaesser, B. & Schacter, D. L. Episodic Empathy: When imagining and remembering increase willingness to help others. (under review at *Proceedings of the National Academy of Sciences, USA*).

Abstract

Empathy plays an important role in human social interaction. A multifaceted construct, empathy includes a prosocial motivation or intention to help others in need. While humans are often willing to help others in need, at times (e.g., during intergroup conflict) empathic responses are diminished or absent. Research examining the cognitive mechanisms underlying prosocial tendencies has focused on the facilitating roles of perspective taking and emotion sharing, but has not previously elucidated the contributions of episodic simulation and memory to facilitating prosocial intentions. Here we investigated whether humans' ability to construct episodes by vividly imagining (episodic simulation) or remembering (episodic memory) specific events also supports a willingness to help others. Three experiments provide evidence for an *episodic empathy effect*: when participants were presented with a situation depicting another person's plight, the act of imagining an event of helping the person or remembering a related past event of helping others increased prosocial intentions to help the present person in need compared to various control conditions. We also observed evidence suggesting that the episodic vividness of constructed events—rather than simply heightened emotional reactions or degree of perspective taking—supports this effect. Our results shed light on a role that episodic simulation and memory can play in fostering empathy, and begin to offer insight into the underlying mechanisms.

Episodic Empathy: When imagining and remembering increase willingness to help others

Prosociality is widespread in nature (de Waal, 2008). Slime molds band together to overcome starvation (Gilbert, Foster, Mehdiabadi, Strassmann, & Queller, 2007), rats assist forcefully restrained cagemates (Bartal, Decety, & Mason, 2011), chimpanzees console distressed partners (Fraser, Stahl, & Aureli, 2008). Nonetheless, humans' prosocial tendencies to collaborate with and help one another far exceed that of other species (Fehr & Fischbacher, 2003; Milinski, Semman, & Krambeck, 2002; Nowak & Highfield, 2011). People band with, assist, and console family and friends, but more strikingly, are willing to help strangers who suffer from plights they have not directly experienced themselves. Why are humans so willing to help others?

One approach to answering this question entails investigating evolutionary mechanisms that select behaviors to increase reproductive success (Hamilton, 1964; Nowak & Sigmund, 2005). Another approach is to delineate the cognitive mechanisms that underlie and promote willingness to help others (empathy; Batson, 2011; Zaki & Ochsner, 2012). The latter strategy has primarily focused on how the ability to adopt the thoughts and feelings of others (perspective taking; Lamm, Batson, & Decety, 2007; Tankersley, Stowe, & Huettel, 2007; Waytz et al., 2012) and the subsequently provoked emotional concern for others' welfare (sympathy) support prosocial tendencies (Decety, 2011; Eisenberg & Miller, 1987). Here we ask whether humans' prosocial tendencies arise not only because they can consider others' thoughts and feelings, but also because they can mentally construct the act of helping. Are humans more inclined to lend a helping hand because they can mentally extend it? Might episodic simulation and memory—the abilities to vividly imagine and remember experiences located in a specific time and place (Schacter et al., 2012; Tulving, 2002)—contribute to a willingness to help others?

Although little is known about the prosocial functions of episodic simulation and memory (D'Argembeau, Renaud, & Van der Linden, 2011; Gaesser, 2013; Schacter, 2012), previous research has shown that elaborate and vividly imagined events increase willingness to interact with unfamiliar others (Husnu & Crisp, 2010; Crisp et al., 2010), and that imagining hypothetical experiences and remembering actual experiences depend on many of the same cognitive and neural processes (D'Argembeau & Van der Linden, 2004; Schacter et al., 2012; Szpunar, 2010). If constructing episodic events facilitates prosocial intentions, then both imagining and remembering helping a person in need should heighten participants' willingness to help. We aimed to evaluate this prediction by examining the extent to which imagining and remembering helping a person in need increased willingness to help compared with merely being exposed to another person's plight and thinking of ways the person could be helped without generating an imagined or remembered episode.

To do so, we recruited adults ($n = 75$) to participate in three experiments that examined reactions to stories adapted from various online media (e.g., Twitter, Tumblr, New York Times) (Coke et al., 1978; Rameson et al., 2011). Participants came into the lab and read a series of brief stories depicting people in need (e.g., locked out of a house, dealing with storm damage, recovering from illness). After reading a story of need, participants completed one of several different tasks. In Experiment 1 ($n = 15$), participants were asked to either (i) complete neutral math problems (*No Helping: Math* condition), or (ii) imagine a vivid scenario of helping the person in need (*Imagine Helping* condition) and then later rated their willingness to help the person in need. Comparing these conditions allowed us to assess whether imagining an episodic helping event facilitates prosocial intentions beyond a baseline reaction to learning about another person's plight.

In Experiment 2, we sought to (i) replicate the basic effect in a larger sample; (ii) gain insight into the underlying cognitive mechanisms by including additional dependent measures, and (iii) rule out alternative hypotheses by using more stringent control conditions. To accomplish these objectives, we doubled our sample size ($n = 30$), removed the math task and added two new experimental tasks in which participants were asked to either (i) focus on the story by considering its journalistic style and online media source (*No Helping: Story* condition) or (ii) estimate how the person could be helped by visualizing a website that the story came from and comments posted on it describing how the person in need could be helped (*Estimate Helping* condition). These conditions were designed to recruit semantic retrieval, social cognition, and generation of helping examples. By contrast, the imagine condition alone required simulating a temporally and contextually specific episode. After reading and reacting to all scenarios, participants were re-presented with the scenarios and rated, on a trial-by-trial basis, their willingness to help the person in need, their emotional experiences, and the sensory detail and coherence of their mental images (for estimate and imagine conditions only; see *Methods and Materials* and *Supplemental Information* for a full list of measures).

In Experiment 3, we recruited a new sample of 30 participants. We repeated the procedures of Experiment 2 with the exception of replacing the *Estimate Helping* condition with remembering a related past event of helping someone in need. In addition to the same dependent measures as in Experiment 2, participants also indicated the similarity of past events with the currently presented scenarios of need. This measure was included because having personally experienced similar episodes in one's past has been shown to increase empathy for others, and therefore the degree of relatedness may modulate prosocial intentions in the current study

(Bluck, Baron, Ainsworth, Gesselman, & Gold, 2013; Hodges, Kiel, Kramer, Veach, & Villanueva, 2009; further details in *Materials and Methods* and *Supporting Information*).

Results

Across three experiments reported here, participants were more inclined to help a person in need after constructing a vivid personal episode of helping that person. We refer to this facilitating effect of episodic simulation and memory on prosocial intentions to help as the *episodic empathy effect*.

Experiment 1

As an initial test of this effect, we examined whether imagining a scenario of helping a person in need would increase the willingness to help that person (*Imagine Helping* condition) compared with a baseline reaction to merely being exposed to a person's plight (*No Helping: Math* condition). This contrast revealed a significant increase in the willingness to help a person in need after imagining helping that person relative to only being exposed to the person's plight ($t(14) = 5.13, p < .001$; see Figure 3.1). This finding suggests that episodic simulation can facilitate prosocial intentions to help others. However, because it is possible that the *Imagine Helping* condition merely elicited more attention to the story of need, we sought to examine the episodic empathy effect under conditions that more tightly controlled for attention to the story of need. Moreover, we sought to evaluate a competing hypothesis that the episodic empathy effect is attributable to conceptually priming participants to think in general about how a person in need could be helped (Macrae & Johnston, 1998; Nelson & Norton, 2005) rather than imagining a specific episodic experience per se.

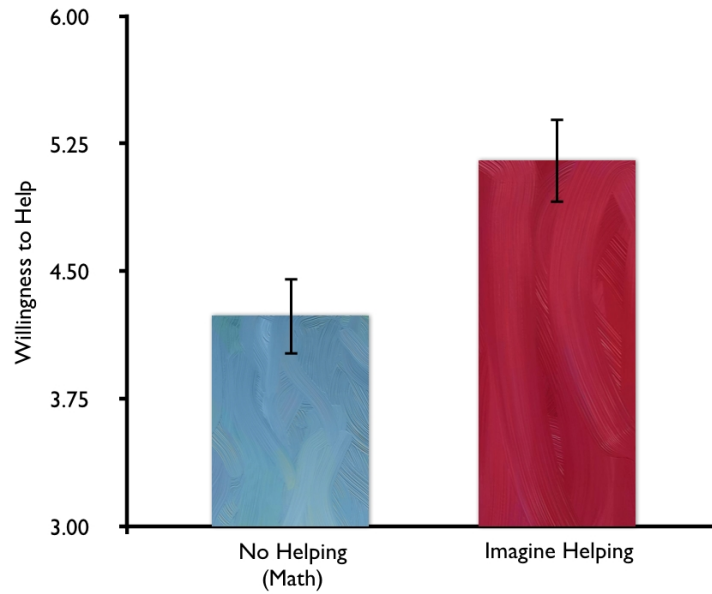


Figure 3.1. Episodic simulation increases willingness to help. Participants were more willing to help (1, not at all willing; 7, very willing) when they imagined an event of helping a person in need (*Imagine Helping*; mean = 5.15, SD = .97) compared with when they were exposed to a person's plight but were prevented from imagining a helping scenario by instead completing neutral math problems (*No Helping: Math*; mean = 4.24, SD = .89) in Experiment 1. This finding suggests that episodic simulation can facilitate empathy. Error bars, mean \pm standard error.

Experiment 2

The results from Experiment 2 further supported an episodic empathy effect (see Figure 3.2a). Participants indicated that they were more willing to help a person in need when they imagined helping the person than when they were exposed to the plight of others by considering the journalistic style and source of the stories of need (*No Helping: Story* condition; $t(29) = 6.68$, $p < .001$), and when they estimated ways a person could be helped by visualizing a website that the story came from and the comments posted on it describing how the person in need could be helped (*Estimate Helping* condition; $t(20) = 5.03$, $p < .001$). Thus, imagining a helping episode promoted intentions to help others to a greater extent than focusing on the story of need or conceptually thinking of ways a person can be helped. Next we consider a potential cognitive mechanism that supports this facilitating effect of episodic simulation on empathy.

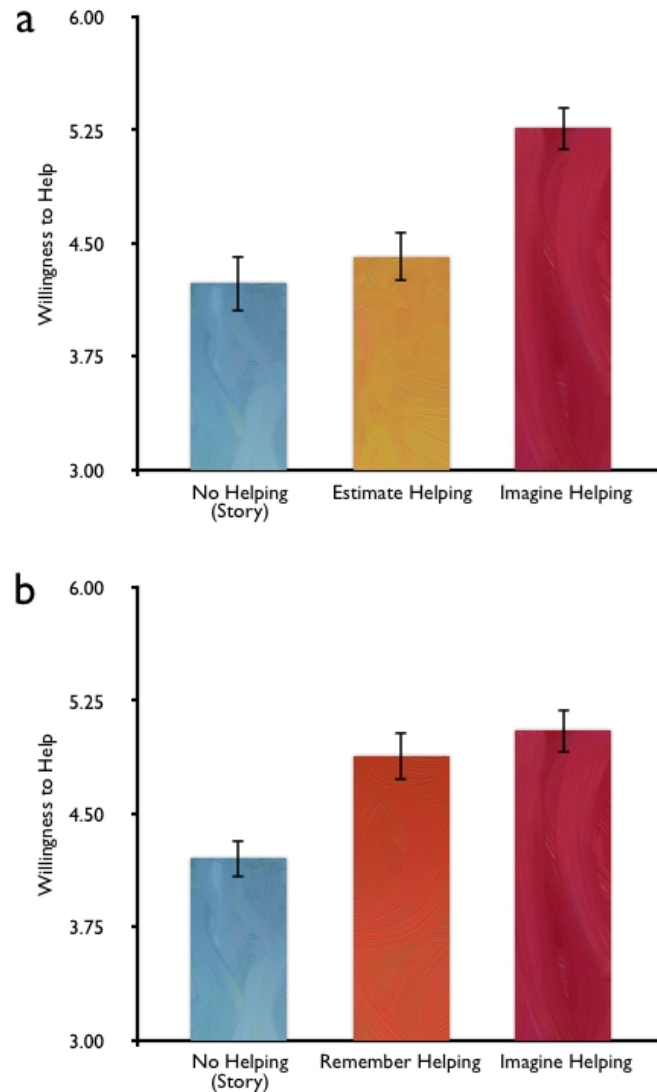


Figure 3.2. Episodic processes (simulation and memory) increase willingness to help. **a**, Imagining a helping event (*Imagine Helping*; mean = 5.26, SD = .81) increased willingness to help (1, not at all willing; 7, very willing) more than focusing on the story of need (*No Helping: Story*; mean = 4.23, SD = 1.0) and estimating how the person could be helped (*Estimate Helping*; mean = 4.41, SD = .92) in Experiment 2. **b**, Both imagining a helping event (*Imagine Helping*; mean = 5.05, SD = .82) and remembering a related helping event (*Remember Helping*; mean = 4.88, SD = .86) increased willingness to help more than focusing on the story of need (*story*; mean = 4.19, SD = .70) in Experiment 3. These findings replicate the episodic empathy effect initially observed in Experiment 1 and extend this effect to remembering related helping events, supporting the hypothesis that episodic process (simulation *and* memory) can facilitate empathy. Error bars, mean \pm standard error.

Perhaps imagining an event increased the episodic vividness of that event relative to the control conditions, which in turn increased the subjective plausibility of the simulated event (Szpunar & Schacter, 2013). As the vividness of an imagined event increases, the event can be brought to mind more easily, and thereby be used as diagnostic knowledge to inform decisions about the plausibility of the simulated event (Tversky & Kahneman, 1973). Consistent with this possibility, previous studies have shown that more elaborately imagined events reduce anxiety, improve intergroup attitudes, and increase intentions to interact with unfamiliar others (Husnu & Crisp, 2010; Crisp et al., 2010). To evaluate the impact of episodic vividness on facilitating prosocial intentions in Experiment 2, we calculated how changes in sensory detail and coherence predicted changes in willingness to help. These analyses revealed that sensory detail and coherence predicted willingness to help when imagining helping a person in need ($r(28) = .43, p = .018$; $r(28) = .47, p = .010$), but did not predict willingness to help in the estimate condition when thinking of ways the person could be helped ($r(28) = .28, p = .133$; $r(28) = .27, p = .148$), (see Figure 3.3a, 3.3b). Although the direction of the correlation is the same in the imagine and estimate conditions, the overall pattern of correlations suggests that it may not be the vividness of imagery alone that underlies the episodic empathy effect, but more specifically, the vividness of imagery for the simulated personal event of helping.

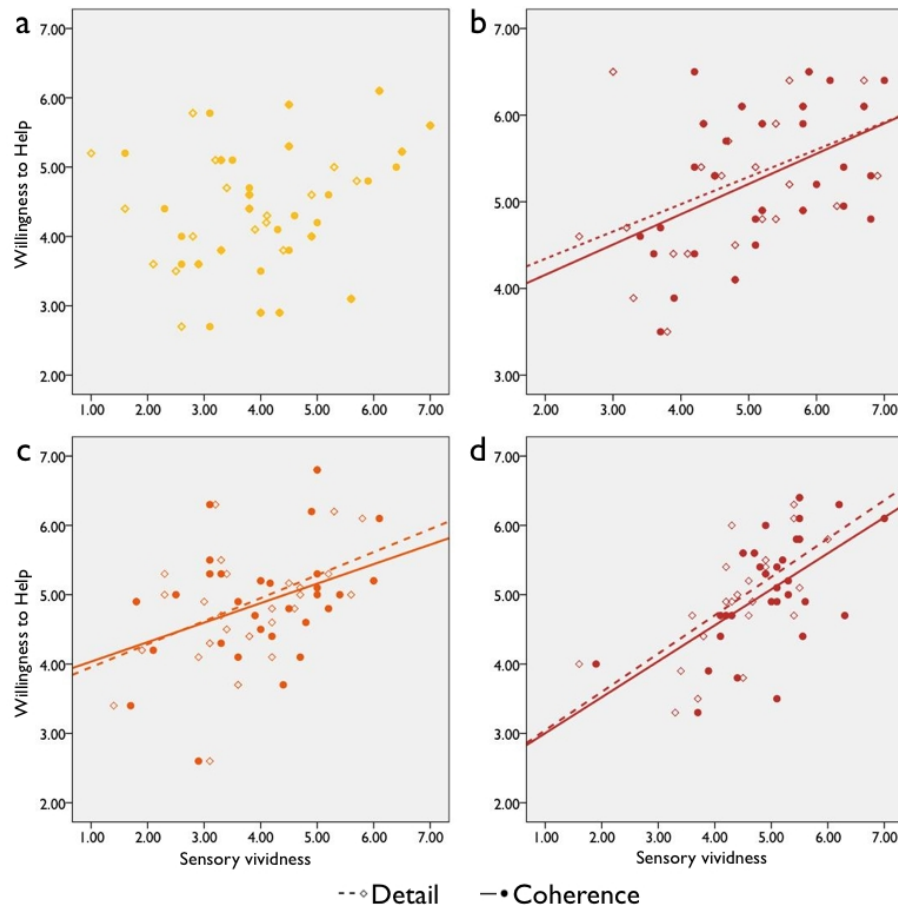


Figure 3.3. Episodic vividness predicts willingness to help. Scatter plots displaying the correlations between willingness to help and sensory vividness for **a**, *Estimate Helping* and **b**, *Imagine Helping* conditions in Experiment 2 and **c**, *Remember Helping* and **d**, *Imagine Helping* conditions in Experiment 3. Sensory detail and coherence predicted willingness to help when participants imagined or remembered a helping event, but did not predict willingness to help when estimating ways the person could be helped by visualizing comments posted on a website depicting how to help the person in need. Thus, it appears that the vividness of episodic helping events -rather than the vividness of imagery in general- predicts willingness to help. Regression lines presented for significant effects.

Such differences could reflect an effect on prosocial intentions that is unique to episodic simulation. Conversely, as noted earlier recent work in psychology and neuroscience suggests that episodic simulation draws on many of the same mental and neural processes as episodic memory (D'Argembeau & Van der Linden, 2004; Schacter et al., 2012; Szpunar, 2010). This observation raises the possibility that the differences shown in Experiment 2 are not uniquely

associated with *imagining* a specific scenario of helping a person in need, but rather arise from explicitly constructing a specific helping scenario -an *episodic* representation– regardless of whether it was imagined or remembered. In Experiment 3, we attempted to distinguish between these competing accounts by determining whether the episodic empathy effect is limited to simulating imagined events or whether it generalizes to episodic remembering of actual events.

Experiment 3

Results from comparing performance in the *Imagine Helping*, *Remember Helping*, and *No Helping: Story* conditions reinforced and extended the findings from Experiment 1 and 2. Participants were more willing to help people in need when they imagined helping the person than when they were merely exposed to the person's plight, ($t(29) = 5.88, p < .001$; see Figure 3.2b). Remembering a past helping experience also increased willingness to help a person in need compared to exposure to the person's plight ($t(29) = 4.88, p < .001$). Notably, imagining helping events did not promote willingness to help to a greater extent than remembering helping events ($t(29) = 1.59, p = .123$). Therefore, the increase in prosocial intentions appears to be similar across episodic memory and episodic simulation. Next, we examined whether this effect operated through similar cognitive mechanisms.

Bolstering the findings from Experiment 2, we again observed evidence that episodic vividness influences willingness to help. We found that more detailed and coherent imagined events were associated with increased willingness to help ($r(28) = .67, p < .001$; $r(28) = .59, p = .001$). Similarly, more detailed and coherent remembered events were also associated with increased willingness to help ($r(28) = .47, p = .009$; $r(28) = .38, p = .039$; see Figure 3.3c, 3.3d). Taken together, these results suggest that the episodic vividness of a constructed event may promote prosocial intentions regardless of whether the helping event is imagined or remembered.

Despite the fact that imagining and remembering fostered episodic empathy to a similar extent, Experiment 3 provided some evidence that imagining produces an advantage in the range of prosocial experiences it facilitates: (i) participants were unable to retrieve helping experiences for several stories, but participants were able to imagine a helping event for all stories (see Figure 3.4), chi-square test of independence ($\chi^2(1, N = 600) = 41.71, p < .001$); (ii) on these “missed” memory trials, willingness to help was reduced to baseline levels; and (iii) the less related a memory was to the present situation of need the less willing the participant was to help ($r(29) = .40, p = .028$). These findings underscore the prosocial utility of episodic simulation: it overcomes the narrowness of past experiences by allowing people to empathize with novel situations they have not directly experienced themselves.

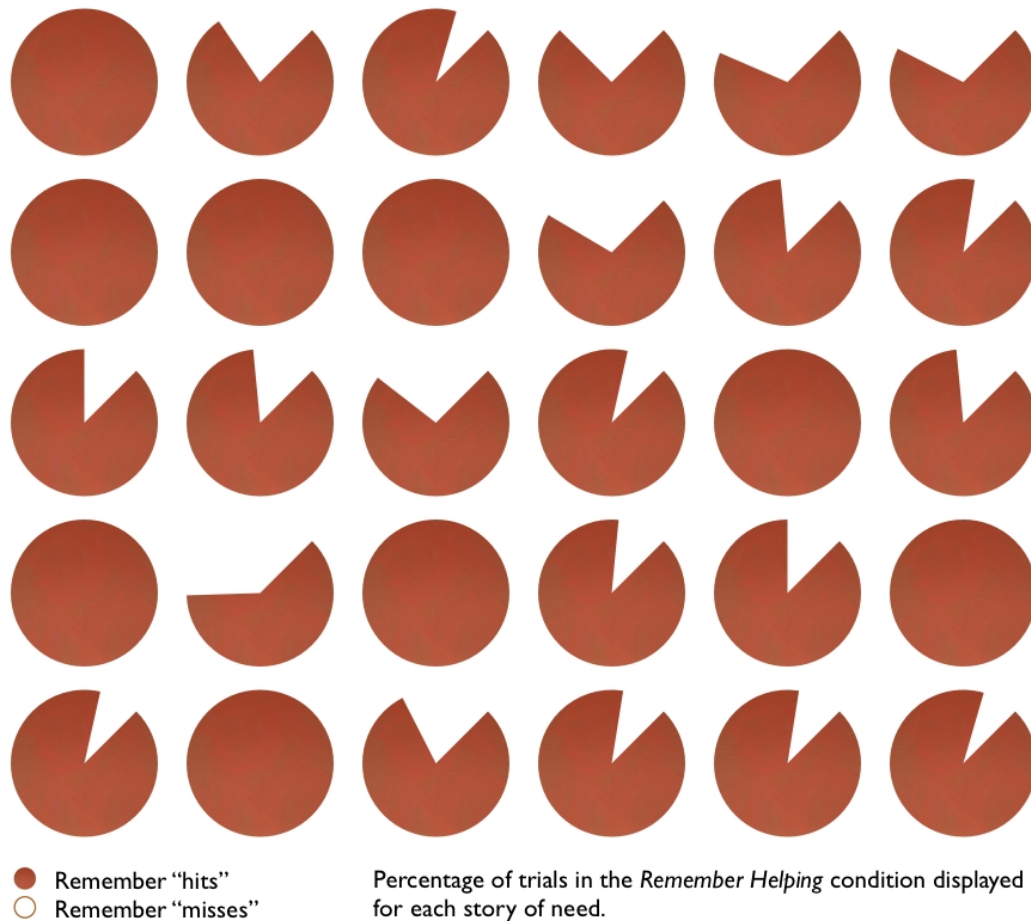


Figure 3.4. The range of the empathic effect of memory is limited. Although imagining and remembering a helping event increased willingness to help to a similar degree, the empathic effect of memory depended on the successful retrieval of related helping events (Remember “hits”) in Experiment 3. Participants were able to imagine, but not remember, a helping event for all trials (Remember “misses”; 39/300 trials collected in the *Remember Helping* condition ranging across 21/30 stories of need). On these failed memory trials, willingness to help was reduced to baseline (mean = 4.27). These findings highlight a flexible advantage of episodic simulation in facilitating empathy for situations of need that have not been personally experienced in the past. Charts displayed for descriptive purposes only.

Perspective Taking

While we have emphasized the role of episodic vividness in underlying the facilitating effect of imagining and remembering on empathy, our previous analyses do not preclude a role of perspective taking in mediating this effect. One possible interpretation of our results is that access to vivid episodic representations does not directly facilitate prosocial intentions; instead, it

may only serve to enhance adopting the thoughts and feelings (i.e. perspective taking) of people in need, which in turn elicits prosocial intentions to help. However, the data do not support this notion. If perspective taking fully accounts for the preferential and parallel increase in willingness to help for episodic processes (i.e. *Imagine Helping* and *Remember Helping* conditions), then perspective taking should significantly differ for estimating and imagining in Experiment 2 and should not differ between imagining and remembering in Experiment 3. In fact, estimating and imagining did not significantly differ with respect to perspective taking ($t(29) = 1.8, p = .075$), whereas imagining and remembering did ($t(29) = 2.46, p = .020$).

Emotional Concern

To assess the role of emotional reactions in supporting prosocial intentions, participants rated the degree to which they experienced 12 different emotions (intrigued; softhearted; troubled; warm; distressed; sympathetic; intent; compassionate; disturbed; tender; moved; worried) for each story of need following the experimental task session. Selected from a subset of emotions measured in past studies, this constellation of emotions was used so as to include a measure of emotional concern within a larger array of emotions, thereby minimizing participants' awareness of this construct (Batson, 2011; Batson, Early, et al., 1997). We did not observe evidence of a consistent relationship between willingness to help and emotional reactions. However, there was some tentative evidence suggesting that the emotion of sympathy may contribute to willingness to help in the current paradigm.

In Experiment 2, there was a trending effect of sympathy for the person in need to predict willingness to help when considering the journalistic style and source of story depicting people in need ($r(28) = .33, p = .075$). However, sympathy did not show a trending effect for willingness to help when estimating ways the person could be helped ($r(28) = .21, p = .278$) or

imagining an episode of helping ($r(28) = .181, p = .338$). In Experiment 3, the relationship between emotion and willingness to help was selective to that of sympathy, as this was the only emotion to significantly predict willingness to help. Sympathy ratings significantly predicted willingness to help when considering the journalistic style and source of stories ($r(28) = .62, p < .001$). There was also a significant effect of sympathy on willingness to help for memory ($r(28) = .52, p = .003$) and, to a lesser extent, when subjects imagined scenarios of helping ($r(28) = .38, p = .039$). This mixed pattern of results across experiments does not allow strong conclusions to be drawn about the relationship between sympathy and willingness to help in the current paradigm. However, it is consistent with previous work finding that sympathy is preferentially evoked by perceived need (Lishner, Batson, & Huss, 2011). While sympathy may play a role in facilitating prosocial intentions, it does not appear to strongly, if at all, contribute to the episodic empathy effect (i.e. the selective increase in willingness to help as a consequence of remembering and imagining events).

Discussion

In three experiments, people increased prosocial intentions when they constructed episodes of helping people in need. Our findings show that these prosocial facilitating effects are difficult to explain in terms of the known prosocial influences of degree of perspective taking or emotional responses and suggest that the episodic vividness of constructed experiences informs our willingness to help others. Although episodic simulation and memory facilitated prosocial intentions to a similar extent, the influence of memory was limited to the successful retrieval of related events, whereas simulation was readily deployed to facilitate prosocial intentions more broadly, including situations that had not been directly and personally experienced.

Our results nicely align with a recent study of attenuated empathic responses in amnesic patients (Beadle et al., 2013). Amnesic patients, suffering damage to the medial temporal lobe, displayed lower levels of trait empathy, were less responsive to empathy inductions, and were less prosocial in a social-economic context (e.g., the Dictator Game) compared to healthy controls. Yet, the cognitive mechanisms underlying these empathic deficits were not directly examined in this study. Given that episodic vividness predicted willingness to help people in need in the experiments we reported here, an intriguing possibility is that amnesic patients' impaired abilities to remember and imagine episodic representations directly affected judgments of empathy, hindering access to diagnostic knowledge that can be used to guide decisions about future helping actions. While this possibility awaits direct empirical investigation, the experiments reported here provide an important starting point for research that could be used to develop new strategies targeted at episodic mechanisms for promoting empathy, as well as to guide research characterizing and improving empathic deficits in patient populations suffering from episodic memory and simulation (Beadle et al., 2013).

Rather than rule out a role of perspective taking or emotional concern in supporting prosocial intentions observed in previous studies, our experiments support past findings, but also build upon them by identifying an additional mechanism to increase prosociality. The pattern of results suggests that a distinction exists between the contributions of episodic simulation and memory to facilitating willingness to help on the one hand and the role of perspective taking on the other, at least in the experiments discussed here. An important direction for future work will be further delineating the relation between episodic and perspective taking processes (Rosenbaum, Stuss, Levine, & Tulving, 2007) in fostering prosocial tendencies.

Moreover, our results also do not eliminate a role for emotions in contributing to the episodic empathy effect. Indeed previous studies have observed that (i) the perceived likelihood that an imagined event will happen has been shown to be selective to emotional experiences (Szpunar & Schacter, 2013), (ii) imagining *positive* social interactions appears to be central to improving attitudes towards and intentions to interact with outgroup members (Crisp & Turner, 2009), and (iii) remembering *good* deeds selectively increases charitable donations (Young, Chakroff, & Tom, 2012). Thus, we suspect that imagining and remembering positively valenced helping interactions may play a role in eliciting the episodic empathy effect.

Humans are an evolutionary success partially because of our ability to collaborate with and help those in need. To the extent that society seeks to foster these socially desirable tendencies, investigating and understanding mental processes that shape empathy is crucial. Several cognitive and emotional mechanisms have already been elucidated and extensively studied by psychology and neuroscience. However, humans may possess at least one more tool that can be used to facilitate prosociality: the ability to construct empathic episodes. By imagining and remembering our own experiences it seems we can come to empathize with the experiences of others.

Materials and Methods

Participants

We recruited a total of 75 participants from a local college (restricted to students under the age of 35) to participate in three experiments described as investigations of their reactions to stories depicting real events adapted from various online media (e.g., Twitter, Tumblr, New York Times) and how these reactions related to different mental abilities (Coke et al., 1978; Rameson

et al., 2011). Participants received \$10 per hour for their participation. All experiments were conducted in compliance with the IRB at Harvard University.

Procedure

After reviewing instructions and completing practice trials (one trial per condition) to ensure task comprehension, participants read 30 stories depicting a person in need presented for 10 seconds each. Following the presentation of each story, participants were pseudo-randomly instructed to complete one of five tasks: (i) complete math problems that involved social interactions unrelated to the story of need (*No Helping: Math*), (ii) consider the journalistic style and online source for stories of need (*No Helping: Story*), (iii) estimate ways the person in need could be helped by visualizing a possible source website and discussion comments that would recommend how the person could be helped (*Estimate Helping*), (iv) imagine an episodic event of helping that person (*Imagine Helping*), or (v) remember a past experience of helping that person (*Remember Helping*). Control conditions were designed to recruit semantic retrieval, social cognition, and generation of helping examples. The *Imagine* and *Remember Helping* conditions alone required constructing a temporally and contextually specific episodic event. Participants had one minute to complete each task for a given trial. Ten trials were presented per condition per experiment. Thus, a total of 20 trials consisting of i and iv were collected for Experiment 1 ($N = 15$, 13 females, mean age = 21.6 standard deviation = 3.0), a total of 30 trials consisting of ii, iii, and iv were collected in the Experiment 2 ($N = 30$, 24 females, mean age = 21.8 standard deviation = 2.9), and a total of 30 trials consisting of i, iv, and v were collected in the Experiment 3 ($N = 30$, 21 females, mean age = 20.3, standard deviation = 2.4).

Next, all the stories were re-presented and participants rated phenomenological experiences including their emotional reactions, sensory qualities of generated trials, and

probability that they would be willing to help the people from the stories on 1-7 Likert scales in a self-paced manner, as well as provide brief descriptions of what ways they thought about, imagined, or remembered helping. Experiment 1 only included a subset of these measures targeted at willingness to help and event descriptions to ensure task compliance. For Experiment 3, in addition to the same dependent measures as in Experiment 2, participants also indicated the similarity of past experiences with the currently presented scenarios of need. This measure was included because having personally experienced similar episodes in one's past has been shown to increase empathy for others, and therefore the degree of relatedness may modulate prosocial intentions in the current study (Bluck et al., 2013; Hodges et al., 2009).

At the conclusion of an experiment, subjects were asked to indicate what the hypotheses were. None indicated as a possible hypothesis that memory or imagination would selectively increase willingness to help others and that this effect would be supported by the vividness of remembered or imagined events. All together, Experiments 2 and 3 each lasted approximately 2 hours in the lab, and Experiment 1 lasted approximately 1.5 hours in the lab. For Experiments 2 and 3, personality trait measures were collected one to two weeks prior to participation, but these did not reveal consistent results across experiments.

General Discussion

The three papers comprising this dissertation examined the contributions of episodic and non-episodic processes to supporting imagined future events, thereby expanding our understanding of the nature of episodic simulation, the processes that inform its expression, and the functions it serves. Specifically, Paper 1 demonstrated that deficits in older adults previously viewed as impairments in episodic imagining and remembering are partially attributable to differences in non-episodic processes; Paper 2 delineated component processes that contribute to imagined events, suggesting that the role of the hippocampus involves actively constructing imagined representations; Paper 3 revealed that episodic simulation and episodic memory can be used to facilitate empathy and hints at a previously unconsidered function of episodic processes in shaping our species' prosocial tendencies.

As such, these papers broadly offer empirical support for recent proposals regarding the structure and function of episodic simulation and episodic memory. As discussed earlier, recent work has established that remembering the past and imagining the future rely on strikingly similar cognitive and neural processes (Addis et al., 2007; Addis et al., 2011; Okuda et al., 2003; Spreng et al., 2009; Szpunar et al., 2007; see, Buckner & Carroll, 2007; Schacter et al., 2012; Szpunar, 2010 for reviews), leading to the proposal that future simulations consist of recombined details stored across episodic memories and require additional constructive processing in order to form coherent hypothetical events (Schacter & Addis, 2007, 2009). By simulating hypothetical future events, we can mentally “test” alternative hypothetical scenarios of what might happen, imagine how selecting different actions would play out, and winnow options down to the preferred outcome. From this perspective, the adaptive value of imagined events mainly draws from informing prediction and planning, while saving the costs of engaging in physical behavior

(Buckner & Carroll, 2007; Ingvar, 1979; Schacter & Addis, 2007, 2009; Schacter et al., 2008; Suddendorf & Corballis, 2007; Tulving, 2005). The papers in this dissertation bolster specific aspects of this foundational work, but more than that, they build on it by expanding and sharpening conceptions of the underlying mechanisms as well as suggesting a novel functional role for episodic simulation.

Paper 1 reported a robust age-related description deficit compared with a modest age-related deficit specific to memory and imagination. In two experiments, we evaluated whether the detail deficits observed for episodic simulation and memory extend to descriptions (i.e., verbal reports) of pictures for everyday scenes—a task that does not explicitly rely on episodic processes, since the picture is presented in front of the participant for the duration of the trial. The largest difference between older and younger adults was on the description task and not the episodic simulation or memory tasks. On the one hand, this study adds to the evidence that a deficit specific to episodic simulation and memory in older adults does indeed exist (Addis et al., 2008; Levine et al., 2002). On the other hand, the evidence from this study should temper interpretations of the size of episodic simulation and memory deficits in older adults and emphasizes the role of non-episodic processes (i.e., narrative style, inhibitory deficits) in mediating these deficits.

Previous observations of hippocampal activity when imagining events could reflect cognitive processes related to the demands of constructing imaginary events, encoding these novel events into memory, novelty detection, or some combination of these processes. Thus, to fully understand the contributions of the hippocampus to episodic simulation, it is important to control for these highly related processes. Using a design that combined an experimental recombination, subsequent memory, and task-switching paradigm, Paper 2 disentangled

component processes recruited for imagining events and evaluated whether these processes are supported by the hippocampus. After accounting for effects of subsequent memory and task novelty, Paper 2 identified a region in the hippocampus that was preferentially activated for newly constructed imagined events. In particular, our data suggest that a specific region within the left lateral posterior hippocampus may uniquely contribute to the construction of imagined future events. These results support the hypothesis that the hippocampus may support several distinct but related processes that are critical for imagining future events (Addis & Schacter, 2012). Moreover, they help to make sense of the aforementioned inconsistencies in the neuropsychological literature, suggesting that the existence and type of deficits in imagining exhibited by a patient with MTL damage may very well depend on the precise subregions of the hippocampus that are damaged and spared (Mullally et al., 2013).

Paper 3 revealed that when participants imagined a specific event of helping a person in need, or remembered a related helping event, they were more willing to express prosocial intentions to help that person. This effect of episodic processes on empathy held after controlling for the degree of considering the thoughts and feelings of the person in need (i.e., perspective taking, theory of mind, or mentalizing), a factor previously shown to modulate willingness to help. The episodic empathy effect is not simply explained by theory of mind or emotional concern, because sensory detail and coherence of the imagined and remembered helping events predicted willingness to help. The more detailed and coherent an episodic event, the more willing participants were to express the intention to help people in need. Although episodic simulation and memory both increased a willingness to help, the effect of episodic simulation on empathy was uniquely flexible. That is, participants were at times unable to remember a related helping event (if they had not experienced a related event in their personal past); however, participants

were able to imagine a helping event for every trial. On these “missed” memory trials, willingness to help remained at baseline levels. These findings suggest a possible flexible, prosocial advantage of episodic simulation over memory: episodic simulation overcomes the narrowness of our personal pasts, allowing us to empathize with people facing novel experiences that differ from our own.

The findings of the three papers comprising this dissertation have a number of implications with theoretical, clinical, and applied significance. For the most part, the implications of each paper are independent of one another. However, there is a clear and intriguing line of research that could arise from drawing on seemingly disconnected findings across papers. Towards the end of my discussion I will delve into the implications that only arise from considering the findings of the papers in tandem.

Theoretical Implications

Papers 1 and 2 add to the growing literature suggesting a tight link between episodic simulation and episodic memory. Paper 1 strengthens claims that specificity deficits in older adults derive—at least in part—from impairments in remembering the past and imagining the future (Addis et al., 2008; Addis et al., 2010; Romero & Moscovitch, 2012). Paper 1 also suggests that in order to fully explain age-related differences in specificity, theoretical models will need to incorporate some aspect of non-episodic processes. Consistent with this notion, Rendell and colleagues (2012) recently contrasted age-related differences when generating atemporal scenarios (similar to those used in Hassabis et al., 2007), narratives that involve moving through a scene, and episodic future events. The researchers showed that older adults produced significantly less detail than young adults across tasks, suggesting that age-related difficulty in imagining episodic future events largely reflects non-episodic differences (e.g.,

narrative style, descriptive ability). However, similar to the findings of Paper 1, the researchers also found evidence that older adults' deficits in imagining future episodic events are exacerbated relative to control tasks. Together, these studies demonstrate that age deficits in remembering the past and imagining the future are mostly attributable to non-episodic processes. More generally, these studies call into question the theoretical interpretation of the similarities between remembering and imagining as evidence of shared episodic mechanisms.

According to the constructive episodic simulation framework, the shared episodic mechanisms hypothesized to support remembering and imagining should be distinguishable from non-episodic processes that support picture description. We recently tested this hypothesis by investigating the impact of an episodic specificity induction on memory, imagination, and picture description in young and older adults (Madore, Gaesser, & Schacter, in press). The results showed that the specificity induction selectively increased episodic detail on subsequent memory and imagination tasks in both young and older adults, but had no effect on a picture description task, and thus dissociated the episodic processes supporting memory and imagination from non-episodic processes recruited for picture description. Considered together with the findings of Paper 1, it seems that while non-episodic processes may largely account for age-related changes in remembering and imagining, episodic processes also provide a distinct contribution to remembering and imagining.

Paper 2 reinforces the hypothesis that the hippocampus contributes to imagining hypothetical events (Addis et al., 2007; Addis & Schacter, 2008; Weiler et al., 2010). More specifically, Paper 2 supports a multifaceted view of the hippocampus: distinct subregions of the hippocampus contribute to recombining details into coherent events, recognizing when imagined events consist of novel information, and encoding these events into memory for later use (Addis

& Schacter, 2012; Szpunar, Addis, McLelland, & Schacter, 2013). Previous work emphasized that the anterior hippocampus may underlie recombination processes. However, based on the results of Paper 2, previous observations of anterior hippocampal activity likely reflect encoding of novel events into episodic memory rather than their construction. Consistent with this interpretation, Martin et al. (2011) recently found that activity in the anterior hippocampus was strongly related to subsequent memory for imagined future events.

While Papers 1 and 2 have theoretical implications regarding the mechanisms underlying imagined events, Paper 3 provides insight into a novel functional account of why humans are equipped with episodic simulation in the first place (Gaesser, 2013). This functional account expands the possible adaptive benefits of episodic simulation from prediction, planning (e.g., “previewing” the outcomes of hypothetical alternative scenarios) and emotional regulation (Schacter, 2012) to now include facilitating prosociality. The adaptive function of facilitating prosociality is not necessarily mutually exclusive with previous functional accounts of episodic simulation. However, given the fundamental role that prosociality is thought to play in driving our species’ evolutionary success (Adolphs, 1999; Dunbar, 1998; Nowak & Highfield, 2011; Rand et al., 2012; Tomasello, 2000; Zaki & Ochsner, 2012), facilitating prosociality likely constitutes one of episodic simulation’s primary advantages.

Clinical Implications

To the extent that Paper 1 demonstrates AI performance in healthy older adults for remembering the past and imagining the future is largely attributed to non-episodic processes, the question remains whether or not other populations with known memory and simulation deficits on the AI will show a similar parallel difference across remembering, imagining, and describing pictures. In the absence of a non-episodic control condition similar to the picture

description task, previously observed memory and imagination deficits could result from broader differences in non-episodic processes (Addis, Sacchetti, et al., 2009; Brown et al., 2013; D'Argembeau, Raffard, et al., 2008; Gamboz et al., 2010; Hassabis, Kumaran, Vann, et al., 2007; Klein et al., 2002; Rasmussen & Berntsen, in press; Tulving, 1985; Williams et al., 1996).

Of particular theoretical interest is the pattern of imagining, remembering, and describing pictures in populations with a selective deficit restricted to the domain of episodic processes. One neuropsychological condition with an isolated episodic deficit and reduced specificity for imagining and remembering is amnesic mild cognitive impairment (aMCI, a precursor to Alzheimer's disease; Gamboz et al., 2010). The restricted impairment in episodic processes, likely the result of hippocampal damage, makes aMCI patients a clinical population well suited for studying the relationship between imagining the future, remembering the past, and describing the present. If episodic specificity deficits in aMCI patients extend beyond generating past and future events to include descriptions of the pictures, then it opens the possibility that the impairment is cognitively less selective than initially conceived. A study by Gaesser et al. (in preparation) using the AI and a design similar to that described in Paper 1 indicates that aMCI patients exhibit impairments in episodic simulation and memory as previously shown (Gamboz et al., 2010), but are also impaired on the picture description task, suggesting that non-episodic processes may also be affected in aMCI. The question now remains whether other patient populations, such as patients with Alzheimer's disease, may show less selective deficits on these measures than previously thought (e.g., Addis, Sacchetti, et al., 2009). This line of work provides a greater understanding of age-related decline in episodic simulation and memory of healthy and pathological older adults and begins to reveal the link between episodic processes and higher-order non-episodic processes (e.g., narrative style, communicative goals) that shape its

expression. Paper 1 will help guide future studies targeted at better characterizing deficits in psychiatric and neurological disorders and in time possibly contribute to developing interventions targeted at these mechanisms.

Similarly, the findings from Paper 3 will also inform the diagnosis and treatment of mental disorders in several ways. First, this research has the potential to identify previously unconsidered cognitive mechanisms involving episodic simulation and memory that may underlie disorders of empathy (e.g., psychopathy, acquired sociopathy). Second, these findings provide the basis for a unique prediction: the severity of deficits in episodic simulation and memory (e.g., amnesic mild cognitive impairment (aMCI) patients and Alzheimer's disease patients) will track with the severity of empathic deficits under certain conditions. For example, patients with mild to moderate memory deficits generate reduced episodic detail when imagining or remembering events; interventions directed at enhancing episodic detail might also be useful in enhancing empathy (Maestas & Rude, 2012; Madore, et al., in press; Neshat-Doost et al., 2012; Rudoy et al., 2009). Third, interventions directed at episodic detail may be especially effective at enhancing empathy in disorders characterized by impairments in perspective taking (or theory of mind) by providing an alternative route to affect empathy (Blair, 2005; Kahn, Byrd, & Pardini, 2013; Young, Koenigs, Kruepke, & Newman, 2012). Paper 3 therefore lays the foundation for work that could one day guide the development of interventions targeted at enhancing empathy via episodic processes with the goal of mitigating empathic deficits observed in mental disorders.

Applied Implications

The findings from Paper 1 showed that specificity deficits in older adults' imagined and remembered events remained after controlling for differences in picture description, suggesting

that older adults' deficits partially reflect impairments selective to episodic processes. As mentioned above, Madore et al. (in press) selectively attenuated specificity deficits in the memory and simulation tasks through specificity inductions that targeted episodic processes. The implications of these findings, however, may extend beyond the domain of memory. Given the known role of episodic processes in supporting everyday functions, an intriguing possibility is that similar kinds of episodic specificity inductions could be applied to help college students perform better on exams (Taylor et al., 1998), older adults solve problems independently (Sheldon et al., 2011; see also Gerlach et al., 2011), and all of us make more farsighted decisions by overcoming temporal discounting (Benoit et al., 2011; Peters & Büchel, 2010).

Expanding on these everyday functions, Paper 3 suggests that episodic processes could be used to foster empathy with implications for increasing socially desirable behavior and significant health benefits. Prosocial interactions are known to improve well-being and self-esteem, educational and occupational achievement, and the ability to independently perform everyday physical activities (i.e., functional ability; Aknin, Hamlin, & Dunn, 2012; Caprara & Steca, 2005; Weinstein & Ryan, 2010; Wilson, 2000). Additional health benefits of behaving prosocially include decreasing school truancy and even increasing overall quality of life (Musick, Herzog, & House, 1999; Wilson, 2000). Research has shown, for example, lower mortality rates among older adults who volunteer, compared to non-volunteers (Musick et al., 1999). The findings from Paper 3 reveal novel cognitive mechanisms for enhancing empathy that could then be used to develop new strategies for promoting social interactions with positive health consequences in everyday life in healthy young and older adults.

It is on this last point where the implications from across papers merge. Paper 1 demonstrates that both remembered and imagined events in older adults are characterized by

reduced episodic detail compared to young adults. Paper 3 revealed that episodic detail predicted willingness to help a person in need. Taken together, a straightforward prediction emerging from these findings is that the facilitating effect of episodic processes on willingness to help will be diminished or absent in older adults depending on the degree of their deficits in episodic detail. In light of the extant literature that decisively shows older adults are more prosocial compared to young adults, this prediction may initially appear counterintuitive (Bailey, Ruffman, & Rendell, 2013; Gruhn, Rebucal, Diehl, Lumley, & Labouvie-Vief, 2008; Richter & Kunzmann, 2011; Sze, Gyurak, Goodkind, & Levenson, 2012). However, these differing perspectives could be easily reconciled if older adults are generally more prosocial based on non-episodic processes (e.g., increased emotional reactivity, or shifts to more social and emotionally meaningful goals); that is, increased prosociality in older adults may exist despite lacking a “prosocial boost” from episodic processes. Pilot studies currently underway in which old and young adults are given a modified version of the procedures described in Paper 3 suggest that this is indeed the case. The next step is to see whether our interventions targeted at enhancing episodic detail (Madore et al., in press) might be used to further enhance empathy in older adults.

Outstanding Questions

In closing this dissertation, I will discuss several outstanding questions that arise from the findings of my papers, questions that reflect what I believe will be the crucial and exciting directions for research to investigate moving forward.

Although a great deal of research has examined the cognitive basis of remembering episodic events, less is known about the nature of imagining episodic events, and almost nothing is known about how the two relate to social decision-making. Paper 3 will serve as the springboard for my future work at the intersection of episodic simulation, memory, and social

decision-making. As an independent investigator, I am most interested in further elucidating the cognitive mechanisms underlying these intertwined processes and applying this knowledge to facilitate socially desirable behavior that promotes mental health. I will therefore focus my discussion in this section on questions that surface from this line of experiments.

Episodic vividness: correlation or causation?

Across three experiments in Paper 3, imagining helping a person in need increased willingness to help that individual relative to control conditions. Though the effect of episodic processes on empathy appears robust, much work is still needed to illuminate the underlying mechanisms. Paper 3 showed that the episodic vividness of imagined helping events predicted a willingness to help people in need: the more detailed and coherent an episodic helping event was, the more willing an individual was to help a person in need. However, episodic vividness was not directly manipulated, and thus it is currently unknown whether episodic vividness *causally* influences, or is merely correlated with, a willingness to help others. Consistent with a causal influence, previous research on intergroup contact has shown that instructing participants to imagine specifically *when* and *where* (two defining features of episodic experiences, Tulving, 2002) they would positively interact with unfamiliar others increased the vividness of an imagined event, and subsequently, increased intentions to interact with unfamiliar others independent of changes in attitude and anxiety (Husnu & Crisp, 2010). Similarly, episodic detail in an imagination-inflation paradigm has been shown to track with the subjective plausibility of imagined events (Szpunar & Schacter, 2013).

To explicitly address this issue, a variety of manipulations drawn from these and related studies known to modulate the degree of episodic vividness could be deployed, while observing the subsequent impact on a willingness to help others. If episodic vividness causally contributes

to facilitating intentions to help others, then experimentally heightening imagined detail and coherence should subsequently increase a willingness to help a person in need. However, if the episodic vividness manipulations do not impact a willingness to help others, such findings would suggest that the facilitating effect of episodic processes on empathy may operate through alternative cognitive mechanisms such as those previously documented (e.g., perspective taking, self-other identity merger, reward processing; Aknin, Sandstrom, Dunn, & Norton, 2011; Batson, et al., 1997; Cialdini, Brown, Lewis, Luce, & Neuberg, 1997; Coke et al., 1978; Decety, 2005; Moll et al., 2006; Mathur et al., 2010; Waytz et al., 2012).

Does perspective taking mediate the effect of episodic processes on empathy?

Is this empathic effect driven solely by access to a vivid episodic representation of helping? Or is this empathic effect mediated in part or in full by enhanced consideration of people's thoughts and feelings (i.e., theory of mind, or mentalizing)? Although perspective taking could not fully account for the increase in willingness to help for episodic processes observed in Paper 3, the results did not rule out the possibility that the empathic effect could partially be attributed to heightened perspective taking. Perhaps episodic simulation and memory facilitate a willingness to help others partially as a result of interactions with theory of mind. For instance, considering a person-in-need's perspective may shape what to imagine in order to most suitably help that individual. Another possibility is that the empathic effect of episodic simulation operates by making the perspective of the person in need more salient. Of particular importance will be designing experiments to disentangle the contributions of episodic processes and perspective taking processes to empathy, revealing the exact boundaries of their independence and possible interaction.

Contemplating the relationship between episodic and perspective taking processes also leads to an intriguing question as to whether or not episodic simulation could enhance empathy in the absence of perspective taking. Is perspective taking *necessary* for episodic simulation to enhance a willingness to help others? While perceiving an unpleasant mental state in another person (De Vignemont & Singer, 2006; Jackson, Meltzoff, & Decety, 2005) may be a necessary cognitive step to elicit helping (Chakroff & Young, in press), it is less clear whether the ability to adopt another person's thoughts and beliefs is required. At this point, we are left to speculate—though I am confident we will not be left speculating for much longer.

Are there empathic asymmetries between episodic simulation and episodic memory?

Imagining and remembering facilitated empathy to a similar degree in Paper 3. While imagining and remembering events rely on many of the same cognitive processes, important differences have also been noted in the literature (Schacter et al., 2012). Paper 3 provided some evidence that episodic vividness plays a role in supporting the effect of both imagining and remembering; however, it is unknown whether differences in the way people imagine and remember asymmetrically support the facilitating effect of simulation and memory on empathy. Three differences are most relevant to the current discussion. First, remembered events are associated with greater perceptual details than imagined events (Berntsen & Bohn, 2010; D'Argembeau & van der Linden, 2004; Johnson et al., 1988; McDonough & Gallo, 2010). Second, people tend to experience more intense emotions when they anticipate future experiences than when they reflect on past experiences (Carsuo, 2010; Van Boven & Ashworth, 2007). Third, imagined future events tend to be even more emotionally positive and idyllic than remembered past events (Berntsen & Bohn, 2010; D'Argembeau & Van der Linden, 2004; Gallo, Korthauer, McDonough, Teshale, & Johnson, 2011; Newby-Clark & Ross, 2003;

Rasmussen & Berntsen, 2013). Such a positivity bias is associated with a heightened sense of imagery, sense of reliving, vividness, and closer temporal distance (Rasmussen & Berntsen, 2013; see Rasmussen & Berntsen, 2009; Wilson, Gunn, & Ross, 2009 for related reviews).

Whether these phenomenological differences in perception and emotion produce asymmetrical effects on empathy remains an open question. Currently, though, we have gained some insight into understanding differences in the range of empathic events episodic simulation and memory can facilitate. Paper 3 highlights a possible flexible advantage of episodic simulation over memory, allowing us to empathize with people facing novel experiences that diverge from our own. Further illumination of the mechanisms underlying this flexible advantage will be an important goal of future work.

Do episodic processes normally support prosociality?

While there is now empirical evidence that episodic processes can be used to facilitate prosocial intentions, this should not be interpreted as evidence that episodic processes will facilitate prosociality in all cases. Indeed, there may be particular cases in which episodic processes could in fact produce the opposite effect and inhibit prosocial intentions. For example, if the contents of imagined and remembered events are focused on how burdensome the required helping actions would be or probable damage to the self, then episodic processes may reduce the likelihood of prosocial intervention. However, I am tentatively encouraged that the scales may tip in favor of facilitating prosociality based on the well-established positivity bias noted in the previous section (Rasmussen & Berntsen, 2009; Wilson et al., 2009)—that is, to the extent that prosocial events are considered positive experiences, they are more likely to be imagined and remembered, and are more likely to be vividly experienced compared to negative experiences. Moreover, remembering *good* deeds has been shown to increase prosocial behavior whereas

remembering *bad* deeds had no effect on behavior (Young et al., 2012). Paper 3 demonstrates that episodic simulation and memory *can* be used to facilitate prosocial intentions, but whether these processes *normally* facilitate prosociality is an open question of great applied and theoretical significance.

Do intentions to help translate into actual helping behavior?

The link between intentions to help and helping behavior is where the theoretical rubber hits the road of everyday life. Can the empathic effect of episodic processes be used to help actual people in need outside of the laboratory? That is, does an increase in prosocial intentions engendered by imagining or remembering a helping event translate into an increase in actual prosocial behavior? Although it may be too arduous to observe participants engaging in everyday prosocial behavior (e.g., repairing broken-down cars, putting out kitchen fires, assisting the elderly), recent studies have begun to successfully gain traction on prosocial behavior by examining donating behaviors (Cuddy, Rock, & Norton, 2007; Milinski et al., 2002; Young et al., 2012). To address this issue, I have developed a novel paradigm in coordination with local charities that seeks to apply episodic processes to helping actual people in need. Specifically, participants imagine or remember helping events using objects that actual people need outside of the laboratory and then participants are given the opportunity to donate these objects to charity.

Conclusion

Research on memory has recently shifted to include imagining the future. Contributing to our understanding of this new landscape, this dissertation investigated the cognitive and neural mechanisms underlying episodic simulation, as well as the functions it serves. Paper 1 uncovered age-related changes in remembering the past, imagining the future, and describing the present in healthy adults. Paper 2 delineated component cognitive and neural processes that contribute to

imagining novel events. Paper 3 revealed a role of imagining and remembering in facilitating prosocial intentions to help people in need.

These findings serve as a starting point for future work on episodic simulation, memory, and empathy in typically functioning young adults, and, importantly, will guide future work targeted at alleviating deficits in older adults and populations afflicted with mental disorders. Indeed, follow-up studies are already underway. I view this dissertation less as a capstone of my work as a graduate student, and more as a beginning of my career as an independent investigator. With any luck, by the time I am a wizened professor, deficits in episodic detail and yet-to-be-discovered deficits in empathy will have been thoroughly examined and addressed. In the meantime, there is much work to do. The future remains a frontier: largely unknown and vast, it awaits and invites investigation. Let us heed the invitation, let us go exploring—memory-erasing mad scientists be damned.

References

- Addis D. R., Cheng T., Roberts R. P., & Schacter D. L. (2011). Hippocampal contributions to episodic simulation of specific and general future events. *Hippocampus*, 21, 1045-1052.
- Addis, D. R., Musicaro, R., Pan, L., & Schacter, D. L. (2010). Episodic simulation of past and future events in older adults: Evidence from an experimental recombination task. *Psychology and Aging*, 25, 369-376.
- Addis, D. R., Pan, L., Vu, M.-A., Laiser, N., & Schacter, D. L. (2009). Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering. *Neuropsychologia*, 47, 2222-2238.
- Addis, D. R., Roberts, R. P., & Schacter, D. L. (2011). Age-related neural changes in autobiographical remembering and imagining. *Neuropsychologia*, 49, 3656-3669.
- Addis, D. R., Sacchetti, D. C., Ally, B. A., Budson, A. E., & Schacter, D. L. (2009). Episodic simulation of future events is impaired in mild Alzheimer's Disease. *Neuropsychologia*. 47, 2660-2671.
- Addis, D. R. & Schacter, D. L. (2008). Effects of detail and temporal distance of past and future events on the engagement of a common neural network. *Hippocampus*, 18, 227-237.
- Addis, D. R. & Schacter, D. L. (2012). The hippocampus and imagining the future: where do we stand? *Frontiers in Human Neuroscience*, 5, 1-12.
- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, 45, 1363-1377.
- Addis, D. R., Wong, A. T., & Schacter, D. L. (2008). Age-related changes in the episodic simulation of future events. *Psychological Science*, 19, 33-41.
- Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Science*, 3, 469-479.
- Aknin, L. B., Hamlin, J. K., & Dunn, E. W. (2012). Giving leads to happiness in young children. *PLOS One*, 7, 39211.
- Aknin, L. B., Sandstrom, G. M., Dunn, E. W., & Norton, M. I. (2011). It's the recipient that counts: Spending money on strong social ties leads to greater happiness than spending on weak social ties. *Plos One*, 6, e17018.
- Allport, G. W. (1954). *The nature of prejudice*. Cambridge, MA: Perseus Books.

- Andelman, F., Hoofen, D., Goldberg, I., Aizenstein, O., & Neufeld, M. Y. (2010). Bilateral hippocampal lesion and a selective impairment of the ability for mental time travel. *Neurocase*, 16, 426-435.
- Anderson, C.A. (1983). Imagination and expectation: The effect of imagining behavioral scripts on personal influences. *Journal of Personality and Social Psychology*, 45, 293-305.
- Anderson, M. C., Ochsner, K. N., Kuhl, B., Cooper, J., Robertson, E., Gabriell, S. W., Glover, G. H., & Gabrielli, J. D. E. (2004). Neural systems underlying the suppression of unwanted memories. *Science*, 303, 232-235.
- Andrews-Hanna, J. R. (2012). The brain's default network and its adaptive role in internal mentation. *Neuroscientist*, 18, 251-270.
- Arbuckle, T. Y., & Gold, D. P. (1993). Aging, inhibition, and verbosity. *Journal of Gerontology: Psychological Sciences*, 48, P225-P232.
- Armitage, C. J. & Reidy, J. G. (2008). Use of mental simulations to change theory of planned behavior variables. *British Journal of Healthy Psychology*, 13, 513-524.
- Atance, C. M. & O'Neill, D. K. (2001). Episodic future thinking. *Trends in Cognitive Science*, 5, 533-539.
- Bailey, P. E., Ruffman, T., & Rendell, P. G. (2013). Age-related differences in social economic decision making: The ultimatum game. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 68, 356-363.
- Bartal, I. B.-A., Decety, J., & Mason, P. (2011). Empathy and Pro-Social Behavior in Rats. *Science*, 334, 1427-1430.
- Bartlett, F. C. (1932). *Remembering*. Cambridge: Cambridge University Press.
- Batson, C. D. (2011). *Altruism in Humans*. New York: Oxford University Press.
- Batson, C. D., Chang, J., & Rowland, J. (2002). Empathy, attitudes, and action: Can feeling for a member of a stigmatized group motivate one to help the group? *Personality and Social Psychology Bulletin*, 28, 1656-1666.
- Batson, C. D., Early, S., & Salvarani, G. (1997). Perspective taking: Imagining how another feels versus imagining how you would feel. *Personality and Social Psychology Bulletin*, 23, 751-758.
- Batson, C. D., Polycarpou, M. P., Harmon-Jones, E., Imhoff, H. J., Mitchener, E. C., Bednar, L. L., Klein, T. R., & Highberger, L. (1997). Empathy and attitudes: Can feeling for a member of a stigmatized group improve feelings toward the group?

- Journal of Personality and Social Psychology*, 72, 105-118.
- Beadle, J. N., Tranel, D., Cohen, N. J., & Duff, M. C. (2013). Empathy in hippocampal amnesia. *Frontiers in Psychology*, 4, 69.
- Benoit, R. G., Gilbert, S. J., & Burgess, P. W. (2011). A neural mechanism mediating the impact of episodic prospection on farsighted decisions. *The Journal of Neuroscience*, 31, 6771-6779.
- Berntsen, D. & Bohn, A. (2010). Remembering and forecasting: The relation between autobiographical memory and episodic future thinking. *Memory & Cognition*, 38, 265-278.
- Blair, R. J. R. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition*, 14, 698-718.
- Bluck, S., Baron, J. M., Ainsworth, S. A., Gesselman, A. N., & Gold, K. L. (2013). Eliciting empathy for adults in chronic pain through autobiographical memory sharing. *Applied Cognitive Psychology*, 27, 81-90.
- Botzung, A., Denkova, E., & Manning, L. (2008). Experiencing past and future personal events: functional neuroimaging evidence on the neural bases of mental time travel. *Brain and Cognition*, 66, 202-212.
- Brown, A. D., Root, J. C., Romano, T. A., Chang, L. J., Bryant, R. A., & Hirst, W. (2013). Overgeneralized autobiographical memory and future thinking in combat veterans with posttraumatic stress disorder. *Journal of Behavior Therapy and Experimental Psychiatry*, 44, 129-134.
- Buckner, R. L. (2010). The role of the hippocampus in prediction and imagination. *Annual Review of Psychology*, 61, 27-48.
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, 1124, 1-38.
- Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, 11, 49-57.
- Caprara, G. V. & Steca, P. (2005). Self-efficacy beliefs as determinants of prosocial behavior conducive to life satisfaction across ages. *Journal of Social and Clinical Psychology*, 24, 191-217.
- Carroll, J. S. (1978). The effect of imagining an event on expectations for the event: An interpretation in terms of availability heuristic. *Journal of Experimental Social*

Psychology, 14, 88-96.

- Carsuo, E. M. (2010). When the future feels worse than the past: A temporal inconsistency in moral judgment. *Journal of Experimental Psychology: General*, 139, 610-624.
- Chakroff, A. & Young, L. (in press). The prosocial brain: perceiving others in need, and acting on it. In L. Padilla-Walker, G. Carlo (eds.), *The Complexities of Raising Prosocial Children: An Examination of the Multidimensionality of Prosocial Behaviors*. New York: Oxford University Press.
- Chua, E., Schacter, D. L., Rand-Giovannetti, E., & Sperling, R. A. (2007). Evidence for a specific role of the anterior hippocampal region in successful associative encoding. *Hippocampus*, 17, 1071-1080.
- Cialdini, R. B., Brown, S. L., Lewis, B. P., Luce, C., & Neuberg, S. L. (1997). Reinterpreting the empathy-altruism relationship: When one into one equals oneness. *Journal of Personality and Social Psychology*, 73, 481-494.
- Cikara, M., Bruneau, E. G., & Saxe, R. R. (2011). Us and them: Intergroup failures of empathy. *Current Directions in Psychological Science*, 20, 149-153.
- Coke, J. S., Batson, C. D., & McDavis, K. (1978). Empathic mediation of helping: A two-stage model. *Journal of Personality and Social Psychology*, 36, 752-766.
- Cooper, J. M., Vargha-Khadem, F., Gadian, D. G., & Maguire, E. A. (2011). The effect of hippocampal damage in children on recalling the past and imagining new experiences. *Neuropsychologia*, 49, 1843-1850.
- Corcoran, R. & Frith, C. D. (2003). Autobiographical memory and theory of mind: Evidence of a relationship in schizophrenia. *Psychology Medicine*, 33, 897-905.
- Coupland, N., & Coupland, J. (1995). Discourse, identity and aging. In J. F. Nussbaum & J. Coupland (eds.), *Handbook of Communication and Aging Research* (pp. 79-103). Hillsdale, NJ: Erlbaum.
- Craik, F. I. M., & Salthouse, T. A. (eds.). (2000). *Handbook of aging and cognition* (2nd ed.). Hillsdale, NJ: Erlbaum.
- Crisp, R. J., Husnu, S., Meleady, R., Stathi, S., & Turner, R. N. (2010). From imagery to intention: A dual route model of imagined contact effects. *European Review of Social Psychology*, 21, 188-236.
- Crisp, R. J. & Turner, R. N. (2009). Can imagined interactions produce positive Perceptions? *American Psychologist*, 64, 231-240.

- Cuddy, A. J. C., Rock, M. S., & Norton, M. I. (2007). Aid in the aftermath of Hurricane Katrina: Inferences of secondary emotions and intergroup helping. *Group Processes & Intergroup Relations*, 10, 107-118.
- D'Argembeau, A., Lardi, C., & Van der Linden, M. (2012). Self-defining future projections: Exploring the identity function of thinking about the future. *Memory*, 20, 110-120.
- D'Argembeau, A., Raffard, S., & Van der Linden, M. (2008). Remembering the past and imagining the future in schizophrenia. *Journal of Abnormal Psychology*, 117, 247-251.
- D'Argembeau, A., Renaud, O., & Van der Linden, M. (2011). Frequency, characteristics, and functions of future-oriented thoughts in daily life. *Applied Cognitive Psychology*, 41, 96-103.
- D'Argembeau, A. & Van der Linden, M. (2004). Phenomenal characteristics associated with projecting oneself back into the past and forward into the future: Influence of valence and temporal distance. *Consciousness & Cognition*, 13, 844-858.
- D'Argembeau, A. & Van der Linden, M. (2006). Individual differences in the phenomenology of mental time travel: the effects of vivid visual imagery and emotion regulation strategies. *Consciousness and Cognition*, 15, 342-350.
- D'Argembeau, A., Xue, G., Lu, Z.L., Van der Linden, M., & Bechara, A. (2008). Neural correlates of envisioning emotional events in the near and far future. *NeuroImage*, 40, 398-407.
- Davis, M. H. (1994). *Empathy: A social psychological approach*. Madison, WI: Brown & Benchmark.
- De Vignemont, F. & Singer, T. (2006). The empathic brain: how, when and why? *Trends in Cognitive Sciences*, 10, 435-441.
- de Waal, F. B. M. (1996). *Good natured: The origins of right and wrong in humans and other animals*. Cambridge, MA: Harvard University Press.
- de Waal, F. B. M. (2008). Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology*, 59, 279-300.
- Decety, J. (2005). Perspective taking as the royal avenue to empathy. In B. F. Malle & S. D. Hodges (eds.), *Other Minds: How Humans Bridge the Divide Between Self and Others*, 135-149. New York: Guilford Press.
- Decety, J. (2011). Dissecting the neural mechanisms mediating empathy. *Emotion Review*, 3, 92-108.

- Depue, B. E., Curran, T., & Banich, M. T. (2007). Prefrontal regions orchestrate suppression of emotional memories via a two-phase process. *Science*, *317*, 215-219.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, *6*, 178-190.
- Duncan, K., Ketz, N., Inati, S. J., & Davachi, L. (2012). Evidence for area CA1 as a match/mismatch detector: a high-resolution fMRI study of the human hippocampus. *Hippocampus*, *22*, 389-398.
- Eisenberg, N. & Miller, P. A. (1987). The relation of empathy to prosocial and related behaviors. *Psychological Bulletin*, *101*, 91-119.
- Epley, N., Caruso, E. M., & Bazerman, M. H. (2006). When perspective taking increases taking: Reactive egoism in social interaction. *Journal of Personality and Social Psychology*, *91*, 872-889.
- Ezzyat, Y. & Davachi, L. (2011). What constitutes an episode in episodic memory? *Psychological Science*, *22*, 243-252.
- Fazio, R. H., Powell, M. C., & Herr, P. M. (1983). Toward a process model of the attitude-behavior relation: Accessing ones attitude upon mere observation of the attitude object. *Journal of Personality and Social Psychology*, *44*, 723-735.
- Fehr, E. & Fischbacher, U. (2003). The nature of human altruism. *Nature*, *425*, 785-791.
- Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences, USA*, *105*, 8557-8562.
- Gaesser, B. (2013). Constructing memory, imagination, and empathy: A cognitive neuroscience perspective. *Frontiers in Psychology*, *3*, 1-6.
- Gallo, D. A., Korthauer, L. E., McDonough, I. M., Teshale, S., & Johnson, E. L. (2011). Age-related positivity effects and autobiographical memory detail: Evidence from a past/future source memory task. *Memory*, *19*, 641-652.
- Gamboz, N., De Vito, S., Brandimonte, M. A., Pappalardo, S., Galeone, F., Iavarone, A., & Della Sala, S. (2010). Episodic future thinking in amnesic mild cognitive impairment. *Neuropsychologia*, *48*, 2091-2097.
- Garry, M., Manning, C., Loftus, E. F., & Sherman, S. J. (1996). Imagination inflation: Imagining a childhood event inflates confidence that it occurred. *Psychological Bulletin and Review*, *3*, 208-214.

- Garry, M. & Polaschek, D. L. L. (2000). Imagination and memory. *Current Directions in Psychological Science*, 9, 6-10.
- Gerlach, K. D., Spreng, R. N., Gilmore, A. W., & Schacter, D. L. (2011). Solving future problems: Default network and executive activity associated with goal-directed mental simulations. *NeuroImage*, 55, 1816-1824.
- Gilbert, D. T., & Wilson, T. D. (2007). Propection: Experiencing the Future. *Science*, 317, 1351-1354.
- Gilbert, O. M., Foster, K. R., Mehdiabadi, N. J., Strassmann, J. E., & Queller, D. C. (2007). High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. *Proceedings of the National Academy of Sciences, USA*, 104, 8913-8917.
- Gold, J. J., Smith, C. N., Bayley, P. J., Shrager, Y., Brewer, J. B., Stark, C. E., Hopkins, R. O., & Squire, L. R. (2006). Item memory, source memory, and the medial temporal lobe: concordant findings from fMRI and memory-impaired patients. *Proceedings of the National Academy of Sciences, USA*, 103, 9351-9356.
- Gollwitzer, P. M. (1999). Implementation intentions: Strong effects of simple plans. *American Psychologist*, 54, 493-503.
- Greenwald, A. G., Carnot, C. G., Beach, R., & Young, B. (1987). Increasing voting-behavior by asking people if they expect to vote. *Journal of Applied Psychology*, 72, 315-318.
- Gregory, W. L., Cialdini, R. B., & Carpenter, K. M. (1982). Self-relevant scenarios as mediators of likelihood estimates and compliance: Does imagining make it so? *Journal of Personality and Social Psychology*, 43, 89-99.
- Gruhn, D., Rebucal, K., Diehl, M., Lumley, M., & Labouvie-Vief, G. (2008). Empathy across the adult lifespan: Longitudinal and experience-sampling findings. *Emotion*, 8, 753-765.
- Hamilton, W. D. Genetical Evolution of Social Behavior 1. (1964). *Journal of Theoretical Biology*, 7, 1-16.
- Hassabis, D., Kumaran, D., & Maguire, E. A. (2007). Using imagination to understand the neural basis of episodic memory. *Journal of Neuroscience*, 27, 14365-14374.
- Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences, USA*, 104, 1726-1731.
- Hassabis, D. & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Sciences*, 11, 299-306.

- Henson, R. (2005). What can functional neuroimaging tell the experimental psychologist? *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, 58, 193-233.
- Hodges, S. D., Kiel, K. J., Kramer, A. D. I., Veach, D., & Villanueva, B. R. (2010). Giving birth to empathy: The effects of similar experience on empathic accuracy, empathic concern, and perceived empathy. *Personality and Social Psychology Bulletin*, 36, 398-409.
- Hoffman, M. L. (1981). Is altruism part of human nature? *Journal of Personality and Social Psychology*, 40, 121-137.
- Hurley, N. C., Maguire, E. A., & Vargha-Khadem, F. (2011). Patient HC with developmental amnesia can construct future scenarios. *Neuropsychologia*, 49, 3620-3628.
- Husnu, S. & Crisp, R. J. (2010). Elaboration enhances the imagined contact effect. *Journal of Experimental Social Psychology*, 46, 943-950.
- Hyman, I. E. & Pentland, J. (1996). The role of mental imagery in creation of false childhood memories. *Journal of Memory and Language*, 35, 101-117.
- Ingvar, D. H. (1979). "Hyperfrontal" distribution of the cerebral grey matter flow in resting wakefulness: On the functional anatomy of the conscious state. *Acta Neurologica Scandinavica*, 60, 12-25.
- Ingvar, D. H. (1985). "Memory of the future": An essay on the temporal organization of conscious awareness. *Human Neurobiology*, 4, 127-136.
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *NeuroImage*, 24, 771-779.
- James, L. E., Burke, D. M., Austin, A., & Hulme, E. (1998). Production and perception of "verbosity" in younger and older adults. *Psychology and Aging*, 13, 355-367.
- Johnson, J. D., McDuff, S. G., Rugg, M. D., & Norman, K. A. (2009). Recollection, familiarity, and cortical reinstatement: a multivoxel pattern analysis. *Neuron*, 63, 697-708.
- Johnson, M. K., Suengas, A. G., Foley, M. A., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General*, 117, 371-376.
- Jones, G. V. (1976). A fragmentation hypothesis of memory: cued recall of pictures and of sequential position. *Journal of Experimental Psychology: General*, 105, 277-

- Kahn, R. E., Byrd, A. L., & Pardini, D. A. (2013). Callous-unemotional traits robustly predict future criminal offending young men. *Law and Human Behavior*, 37, 87-97.
- Kerchner, G. A., Hess, C. P., Hammond-Rosenbluth, K. E., Xu, D., Rabinovici, G. D., Kelley, D. A. C., Vigneron, D. B., Nelson, S. J., & Miller, B. L. (2010). Hippocampal CA1 apical neuropil atrophy in mild Alzheimer disease visualized with 7-T MRI. *Neurology*, 75, 1381-1387.
- Kirwan, C. B. & Stark, C. E. (2004). Medial temporal lobe activation during encoding and retrieval of novel face-name pairs. *Hippocampus*, 14, 919-930.
- Klein, S. B., Loftus, J., & Kihlstrom, J. F. (2002). Memory and temporal experience: The effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Social Cognition*, 20, 353-379.
- Klein, S. B., Robertson, T. E., & Delton, A. W. (2010). Facing the future: memory as an evolved system for planning future acts. *Memory and Cognition*, 38, 13-22.
- Klein, S. B., Robertson, T. E., & Delton, A. W. (2011). The future-orientation of memory: planning as a key component mediating the high levels of recall found with survival processing. *Memory*, 19, 121-139.
- Kumaran, D. & Maguire, E. A. (2007). Match-mismatch processes underlie human hippocampal responses to associative novelty. *Journal of Neuroscience*, 27, 8517-8524.
- Labouvie-Vief, G. & Blanchard-Fields, I. (1982). Cognitive aging and psychological growth. *Aging and Society*, 2, 183-209.
- Lamm, C., Batson, C. D., & Decety, J. (2007) The neural substrate of human empathy: effects of perspective-taking and cognitive appraisal. *Journal of Cognitive Neuroscience*, 19, 42-58.
- Lee, K. H., Farrow, T. F. D., Spence, S. A., & Woodruff, P. W. R. (2004). Social cognition, brain networks and schizophrenia. *Psychological Medicine*, 34, 391-400.
- Lepage, M., Habib, R., & Tulving, E. (1998). Hippocampal PET activations of memory encoding and retrieval: the HIPER model. *Hippocampus*, 8, 313-322.
- Levine, B., Svoboda, E., Hay, J. F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: dissociating episodic from semantic retrieval. *Psychology & Aging*, 17, 677-689.
- Levine, B., Svoboda, E., Turner, G. R., Mandic, M., & Mackey, A. (2009). Behavioral

- and functional neuroanatomical correlates of anterograde autobiographical memory in isolated retrograde amnesic patient M. L. *Neuropsychologia*, 47, 2188-2196.
- Liang, J. C., Wagner, A. D., & Preston, A. R. (2013). Content representation in the human medial temporal lobe. *Cerebral Cortex*, 23, 80-96.
- Libby, L. K., Shaeffer, E. M., Eibach, R. P., & Slemmer, J. A. (2007). Picture yourself at the polls: visual perspective in mental imagery affects self-perception and behavior. *Psychological Science*, 18, 199-203.
- Lishner, D. A., Batson, C. D., & Huss, E. (2011). Tenderness and sympathy: Distinct empathic emotions elicited by different forms of need. *Personality and Social Psychology Bulletin*, 37, 614-625.
- Loftus, E. F. (2003). Make-believe memories. *American Psychologist*, 58, 867-873.
- Loftus, E. F. (2005). Planting misinformation in the human mind: A 30-year investigation of the malleability of memory. *Learning & Memory*, 12, 361-366.
- Loftus, E. F. & Palmer, J. C. (1974). Reconstruction of automobile destruction: Example of interaction between language and memory. *Journal of Verbal Learning and Verbal Behavior*, 13, 585-589.
- Lombardo, M. V., Barnes, J. L., Wheelwright, S. J., & Baron-Cohen, S. (2007). Self-referential cognition and empathy in Autism. *PLoS ONE*, 2, e883.
- Macrae, C. N. & Johnston, L. (1998). Help, I need somebody: Automatic action and inaction. *Social Cognition*, 16, 400-417.
- Madore, K. P., Gaesser, B., & Schacter, D. L. (in press). Constructive episodic simulation: Dissociable effects of a specificity induction on remembering, imagining, and describing in young and older adults. *Journal of Experimental Psychology: Learning, Memory, and Cognition*.
- Maestas, K. L. & Rude, S. S. (2012). The benefits of expressive writing on autobiographical memory specificity: A randomized controlled trial. *Cognitive Therapy and Research*, 36, 234-246.
- Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences, USA*, 97, 4398-4403.
- Maguire, E. A. & Hassabis D. (2011). Role of the hippocampus in imagination and future thinking. *Proceedings of the National Academy of Sciences, USA*, 108, 39.

- Maguire, E. A., Vargha-Khadem, F., & Hassabis, D. (2010). Imagining fictitious and future experiences: Evidence from developmental amnesia. *Neuropsychologia*, *48*, 3179-3186.
- Martin, V. C., Schacter, D. L., Corballis, M., & Addis, D. R. (2011). A role for the hippocampus in encoding simulations of future events. *Proceedings of the National Academy of Sciences, USA*, *108*, 13858-13863.
- Masten, C. L., Morelli, S. A., & Eisenberger, N. I. (2011). An fMRI investigation of empathy for “social pain” and subsequent prosocial behavior. *NeuroImage*, *55*, 381-388.
- Mathur, V. A., Harada, T., Lipke, T., & Chiao, J. Y. (2010). Neural basis of extraordinary empathy and altruistic motivation. *Neuroimage*, *51*, 1468-1475.
- Mazzoni, G. & Memon, A. (2003). Imagination can create false autobiographical memories. *Psychological Science*, *14*, 186-188.
- McDonough, I. M. & Gallo, D. A. (2010). Separating past and future autobiographical events in memory: Evidence for a reality monitoring asymmetry. *Memory & Cognition*, *38*, 3-12.
- McKinnon, M. K., Black, S. E., Miller, B., Moscovitch, M., & Levine, B. (2006). Autobiographical memory in semantic dementia: Implications for theories of limbic-neocortical interaction in remote memory. *Neuropsychologia*, *44*, 2421-2429.
- Melis, A. P. & Semmann, D. (2010). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*, 2663-2674.
- Milinski, M., Semmann, D., & Krambeck, H. (2002). Donors to charity gain in both indirect reciprocity and political reputation. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *269*, 881-883.
- Mitchell, J. P. (2009). Social psychology as a natural kind. *Trends in Cognitive Sciences*, *13*, 246-251.
- Morewedge, C. K., Gilbert, D. T., & Wilson, T. D. (2005). The least likely of times: How remembering the past biases forecasts of the future. *Psychological Science*, *16*, 626-620.
- Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. *Proceedings of the National Academy of Science, USA*, *103*, 15623-15628.
- Murphy, K. J., Troyer, A. K., Levine, B., & Moscovitch, M. (2008). Episodic, but not

- semantic, autobiographical memory is reduced in amnesic mild cognitive impairment. *Neuropsychologia*, 46, 3116-3123.
- Mullally, S. L., Hassabis, D., & Maguire, E. A. (2012). Scene construction in amnesia: an fMRI study. *Journal of Neuroscience*, 32, 5646-5653.
- Musick, M. A., Herzog, A. R., & House, J. S. (1999). Volunteering and mortality among older adults: Findings from a national sample. *Journals of Gerontology Series B-Psychological Sciences and Social Sciences*, 54, S173-S180.
- Nelson, L. D. & Norton, M. I. (2005). From student to superhero: Situational primes shape future helping. *Journal of Experimental Social Psychology*, 41, 423-430.
- Neshat-Doost, H. T., Dalgleish, T., Yule, W., Kalantari, M., Ahmadi, S. J., Dyregrov, A., & Jobson, L. (2012). Enhancing autobiographical memory specificity through cognitive training: An intervention for depression translated from basic science. *Clinical Psychological Science*, 20, 1-9.
- Newby-Clark, I. R. & Ross, M. (2003). Conceiving the past and future. *Personality and Social Psychology Bulletin*, 29, 807-818.
- Nowak, M. A. & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, 437, 1291-1298.
- Nowak, M. A. & Highfield, R. (2011). *Supercooperators: Altruism, Evolution, and Why We Need Each Other to Succeed*. New York: Simon and Schuster.
- Okuda, J., Fujii, T., Ohtake, H., Tsukiura, T., Tanji, K., Suzuki, K., ... Yamadori, A. (2003). Thinking of the future and the past: The roles of the frontal pole and the medial temporal lobes. *Neuroimage*, 19, 1369-1380.
- Perry, D., Hendler, T., & Shamay-Tsoory, S. G. (2011). Projecting memories: the role of the hippocampus in emotional mentalizing. *Neuroimage*, 54, 1669-1676.
- Peters, J. & Büchel, C. (2010a). Episodic future thinking reduces reward delay discounting through an enhancement of prefrontal-mediotemporal interactions. *Neuron*, 66, 138-148.
- Pettigrew, T. F. & Tropp, L. R. (2006). A meta-analytic test of intergroup contact theory. *Journal of Personality and Social Psychology*, 90, 751-783.
- Piliavin, J. A., Dovidio, J. F., Gaertner, S. L., & Clark, R. D. III (1981). *Emergency intervention*. New York: Academic Press.
- Poppenk, J., Evensmoen, H. R., Moscovitch, M., & Nadel, L. (2013). Long-axis specialization of the human hippocampus. *Trends in Cognitive Sciences*, 17, 230-

- Premack, D. & Woodruff, G. (1978). Does the chimpanzee have theory of mind? *Behavioral and Brain Sciences*, 1, 515-526.
- Rabin, J. S. & Rosenbaum, R. S. (2012). Familiarity modulates the functional relationship between theory of mind and autobiographical memory. *Neuroimage*, 62, 520-529.
- Race, E., Keane, M. M., & Verfaellie, M. (2011). Medial temporal lobe damage causes deficits in episodic memory and episodic future thinking not attributable to deficits in narrative construction. *Journal of Neuroscience*, 31, 10262-10269.
- Rand, D. G., Greene, J. D., & Nowak, M. A. (2012). Spontaneous giving and calculated greed. *Nature*, 489, 427-430.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences, USA*, 98, 676-682.
- Rameson, L. T., Morelli, S. A., & Lieberman, M. D. (2011). The neural correlates of empathy: experience, automaticity, and prosocial behavior. *Journal of Cognitive Neuroscience*, 24, 235-245.
- Rasmussen, A. S. & Berntsen, D. (2009). Emotional valence and the functions of autobiographical memories: Positive and negative memories serve different functions. *Memory & Cognition*, 37, 477-492.
- Rasmussen, A. S. & Berntsen, D. (2013). The reality of past versus the ideality of the future: emotional valence and functional difference between past and future mental time travel. *Memory & Cognition*, 41, 187-200.
- Rasmussen, K. W. & Berntsen, D. (in press). Autobiographical memory and episodic future thinking after moderate to severe traumatic brain injury. *Journal of Neuropsychology*, doi: 10.1111/jnp.12003.
- Rendell, P. G., Bailey, P. E., Henry, J. D., Phillips, L. H., Gaskin, S., & Kliegel, M. (2012). Older adults have greater difficulty imagining future rather than atemporal experiences. *Psychology and Aging*, 27, 1089-1098.
- Richter, D. & Kunzmann, U. (2011). Age differences in three facets of empathy: performance-based evidence. *Psychology and Aging*, 26, 60-70.
- Rizio, A. A. & Dennis, N. A. (2013). The neural correlates of cognitive control: successful remembering and intentional forgetting. *Journal of Cognitive Neuroscience* 25, 297-312.

- Romero, K. & Moscovitch, M. (2012). Episodic memory and event construction in aging and amnesia. *Journal of Language and Memory*, 67, 270-284.
- Rosenbaum, R. S., Gilboa, A., Levine, B., Winocur, G., & Moscovitch, M. (2009). Amnesia as an impairment of detail generation and binding: Evidence from personal, fictional, and semantic narratives in K.C. *Neuropsychologia*, 47, 2181-2187.
- Rosenbaum, R. S., Stuss, D. T., Levine, B., & Tulving, E. (2007). Theory of mind is independent of episodic memory. *Science*, 318, 1257.
- Rudoy, J. D., Weintraub, S., & Paller, K. A. (2009). Recall of remote episodic memories can appear deficient because of a gist-based retrieval orientation. *Neuropsychologia*, 47, 948-951.
- Schacter, D. L. (1999). The seven sins of memory: Insights from psychology and cognitive neuroscience. *American Psychologist*, 54, 182-203.
- Schacter, D. L. (2012). Adaptive constructive processes and the future of memory. *American Psychologist*, 67, 603-613.
- Schacter, D. L. & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philosophical Transactions of the Royal Society of London*, 362, 773-786.
- Schacter, D. L. & Addis, D. R. (2009). On the nature of medial temporal lobe contributions to the constructive simulation of future events. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 364, 1245-1253.
- Schacter, D. L., Addis, D. R., & Buckner, R. L. (2007). The prospective brain: Remembering the past to imagine the future. *Nature Reviews Neuroscience*, 8, 657-661.
- Schacter, D. L., Addis, D. R., & Buckner, R. L. (2008). Episodic simulation of future events: concepts, data, and applications. *Annals of the New York Academy of Sciences*, 1124, 39-60.
- Schacter, D. L., Addis, D. R., Hassabis, D., Martin, V. C., Spreng, R. N., & Szpunar, K. K. (2012). The future of memory: remembering, imagining, and the brain. *Neuron*, 76, 677-694.
- Schacter, D. L., Gaesser, B., & Addis, D. R. (2010). Age-related changes in the episodic simulation of past and future events. In A. S. Benjamin (Ed.) *Successful remembering and successful forgetting: A Festschrift in honor of Robert A. Bjork* (pp. 505-525). New York: Psychology Press.
- Schacter, D. L., Gaesser, B., & Addis, D. R. (2013). Remembering the past and

- imagining the future in the elderly. *Gerontology*, 59, 143-151.
- Schacter, D. L. & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus*, 9, 7-24.
- Sheldon, S., McAndrews, M. P., & Moscovitch, M. (2011). Episodic memory processes mediated by the medial temporal lobes contribute to open-ended problem solving. *Neuropsychologia*, 49, 2439-2447.
- Sherman, R. T. & Anderson, C. A. (1987). Decreasing premature termination from psychotherapy. *Journal of Social and Clinical Psychology*, 5, 298-312.
- Sherman, S. J., Cialdini, R. B., Schwartzman, D. F., & Reynolds, K. D. (1985). Imagining can heighten or lower the perceived likelihood of contracting a disease. *Personality and Social Psychology Bulletin*, 11, 118-127.
- Spaniol, J., Davidson, P. S., Kim, A. S., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-related fMRI studies of episodic encoding and retrieval: meta-analyses using activation likelihood estimation. *Neuropsychologia*, 47, 1765-1779.
- Spreng, R. N. & Levine, B. (2006). The temporal distribution of past and future autobiographical events across the lifespan. *Memory and Cognition*, 34, 1644-1651.
- Spreng, R. N., Mar, R. A., & Kim, A. S. N. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience*, 21, 489-510.
- Squire, L. R., Van der Horst, A. S., McDuff, S. G. R., Frascino, J. C., Hopkins, R. O., & Mauldin, K. N. (2010). Role of the hippocampus in remembering the past and imagining the future. *Proceedings of the National Academy of Sciences, USA*, 107, 19044-19048.
- Stotland, E. (1969). Exploratory investigations into empathy. In L. Berkowitz (ed.), *Advances in experimental social psychology*. New York: Academic Press.
- Suddendorf, T. & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic Social and General Psychology Monographs*, 123, 133-167.
- Suddendorf, T. & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel and is it unique to humans? *Behavioral and Brain Sciences*, 30, 299-313.
- Sze, J. A., Gyurak, A., Goodkind, M. S., & Levenson, R. W. (2012). Greater emotional empathy and prosocial behavior in late life. *Emotion*, 12, 1129-1140.

- Szpunar, K. K. (2010). Episodic future thought: An emerging concept. *Perspectives on Psychological Science*, 5, 142-162.
- Szpunar, K. K., Addis, D. R., McLelland, V., & Schacter, D. L. (2013). Memories of the future: New insights into the adaptive value of episodic memory. *Frontiers in Behavioral Neuroscience*, 7, Article 47.
- Szpunar, K. K., Addis, D. R., & Schacter, D. L. (2012). Memory for emotional simulations: Remembering a rosy future. *Psychological Science*, 23, 24-29.
- Szpunar, K. K. & McDermott, K. B. (2008). Episodic future thought and its relation to remembering: Evidence from ratings of subjective experience. *Consciousness & Cognition*, 17, 330-334.
- Szpunar, K. K. & Schacter, D. L. (2013). Get real: Effects of repeated simulation and emotion on the perceived plausibility of future experiences. *Journal of Experimental Psychology: General*, 142, 323-327.
- Szpunar K. K., St. Jacques P. L., Robbins C. A., Wig G. S., & Schacter D. L. (in press). Repetition-related reductions in neural activity reveal component processes of mental simulation. *Social, Cognitive, and Affective Neuroscience*. doi: 10.1093/scan/nst035.
- Szpunar K. K., Watson J. M., & McDermott K. B. (2007). Neural substrates of envisioning the future. *Proceedings of the National Academy of Science, USA*, 104, 642-647.
- Tankersley, D., Stowe, C. J. & Huettel, S. A. (2007). Altruism is associated with an increased neural response to agency. *Nature Neuroscience*, 10, 150-151.
- Taylor, S. E., Pham, L. B., Rivkin, I. D., & Armor, D. A. (1998). Harnessing the imagination: Mental simulation, self-regulation, and coping. *American Psychologist*, 53, 429-439.
- Taylor, S. E. & Schneider, S. K. (1989). Coping and the simulation of events. *Social Cognition*, 7, 174-194.
- Tomasello, (2000). *The Cultural Origin of Human Cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M. & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Trunk, D. L. & Abrams, L. (2009). Do younger and older adults' communicative goals influence off-topic speech in autobiographical narratives? *Psychology and Aging*, 24, 324-337.

- Tulving, E. (1972). Episodic and semantic memory. In E. Tulving, W. Donaldson (eds.), *Organization of Memory*, 381-403. New York: Academic.
- Tulving, E. (1983). Ecphoric processes in episodic memory. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 302, 361-371.
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychologist*, 25, 1-12.
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, 53, 1-25.
- Tulving, E. (2005). Episodic memory and autonoesis: Uniquely human? In H. S. Terrace & J. Metcalfe (eds), *The missing link in cognition: Origins of self-reflective consciousness*, 3-56. Oxford, England: Oxford University Press.
- Turner, R. N., Crisp, R. J., & Lambert, E. (2007). Imagining intergroup contact can improve intergroup attitudes. *Group Processes & Intergroup Relations*, 10, 427-411.
- Tversky, A. & Kahneman, D. (1973). Availability heuristic for judging frequency and probability. *Cognitive Psychology*, 5, 207-232.
- Van Boven, L. & Ashworth, L. (2007). Looking forward, looking back: Anticipation is more evocative than retrospection. *Journal of Experimental Psychology: General*, 136, 289-300.
- van Mulukom, V., Schacter, D. L., Corballis, M. C., & Addis, D. R. (2013). Re-imaging the future: Repetition decreases hippocampal involvement in future simulation. *PLoS One*, 8, e69596.
- Viard, A., Desgranges, B., Eustache, F., & Piolino, P. (2012). Factors affecting medial temporal lobe engagement for past and future episodic events: an ALE meta-analysis of neuroimaging studies. *Brain and Cognition*, 80, 111-125.
- Wagner A. D., Schacter D. L., Rotte M., Koutstaal W., Maril A., Dale A. M., & Buckner R. L. (1998). Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, 281, 1188-1191.
- Waytz, A., Zaki, J., & Mitchell, J. P. (2012). Response of dorsomedial prefrontal cortex predicts altruistic behavior. *Journal of Neuroscience*, 32, 7646-7650.
- Weiler J. A., Suchan B., & Daum I. (2010). Foreseeing the future: occurrence probability of imagined future events modulates hippocampal activation. *Hippocampus*, 20, 685-690.
- Weinstein, N. & Ryan, R. M. (2010). When helping helps: Autonomous motivation for prosocial behavior and its influence on well-being for the helper and recipient. *Journal of Personality and Social Psychology*, 98, 222-244.

- Williams, J. M., Ellis, N. C., Tyers, C., Healy, H., Rose, G., & MacLeod, A. K. (1996). The specificity of autobiographical memory and imageability of the future. *Memory and Cognition*, 24, 116-125.
- Wilson, J. (2000). Volunteering. *Annual Review of Sociology*, 26, 215-240.
- Wilson, A. E., Gunn, G. R., & Ross, M. (2009). The role of subjective time in identity regulation. *Applied Cognitive Psychology*, 23, 1164-1178.
- Wylie, G. R., Foxe, J. J., & Taylor, T. L. (2008). Forgetting as an active process: an fMRI Investigation of item-method-directed forgetting. *Cerebral Cortex*, 18, 670-682.
- Yassa, M. A. & Stark C. E. L. (2008). Multiple signals of recognition memory in the medial temporal lobe. *Hippocampus*, 18, 945-954.
- Young, L., Chakroff, A., & Tom, J. (2012). Doing good leads to more good: The reinforcing power of a moral self-concept. *Review of Philosophy and Psychology*, 3, 325-334.
- Young, L., Koenigs, M., Kruepke, M., & Newman, J. P. (2012). Psychopathy increases perceived moral permissibility of accidents. *Journal of Abnormal Psychology*, 121, 659-667.
- Zacks, R. T. & Hasher, L. (1994). Directed ignoring: Inhibitory regulation of working memory. In D. Dagenbach & T. H. Carr (eds.), *Inhibitory Processes in Attention, Memory, and Language* (pp. 241–264). San Diego, CA: Academic Press.
- Zaki, J. & Ochsner, K. (2012). The neuroscience of empathy: progress, pitfalls and promise. *Nature Neuroscience*, 15, 675-680.

Appendix

Supplementary Information

Methods. Participants who only provided partial data, inappropriate responses (e.g., by providing responses for trials from the *Imagine Helping* and *No Helping: Story* conditions to a question explicitly restricted to trials only from the *Remember Helping* condition), or neglected to provide brief descriptions of what they generated for each task were not considered for data analysis. Two participants were excluded from data analysis in Experiment 3: one participant responded at ceiling for willingness to help across conditions, another participant indicated feeling no emotional reactions at all. However, including these outlining participants did not significantly affect the primary findings: (i) willingness to help was greater for the *Imagine Helping* condition compared to the *No Helping: Story* condition ($t(31) = 4.64, p < .001$), (ii) willingness to help was greater for the *Remember Helping* condition compared to the *No Helping: Story* ($t(31) = 3.29, p = .003$), and (iii) willingness to help did not significantly differ between *Imagine Helping* and *Remember Helping* conditions ($t(25) = .12, p = .909$).

Materials: Episodic vividness. To evaluate the extent that episodic vividness predicted prosocial intentions to help, we included measures of episodic detail and coherence using the following scales:

Detail

The imagined/remembered scene in your mind was? (1 = simple, 4 = moderately, 7 = detailed).

Coherence

The imagined/remembered scene in your mind was (1 = vague, 4 = moderately, 7 = coherent and clear).

Similarly, for the *Estimate Helping* condition, participants were asked:

Detail

The imagined media website in your mind was? (1 = simple, 4 = moderately, 7 = detailed).

Coherence

The imagined media website in your mind was (1 = vague, 4 = moderately, 7 = coherent and clear).

In the second experiment, we included an additional measure of episodic vividness: event pre/re-living.

How strongly did you experience the imagined/remembered event in your mind? (1 = not at all, 4 = moderately, 7 = vividly, as if you were there)

Further supporting the detail and coherence findings, analyses revealed that the strength of pre-living predicted willingness to help after imagining helping a person in need ($r(28) = .54, p = .002$), and re-living predicted willingness to help after remembering a past experience related to the circumstances of the present person in need ($r(28) = .48, p = .008$).

Materials: Example Stories. We provide below a few stories used to depict people in need. Scenarios depicted a variety of situations, and the person in need was presented anonymously so as to minimize possible gender or group membership effects. All of stories are available from the authors upon request.

This person's dog has not returned home in the last 24 hours.

This person is locked out of their house.

While riding the train, this person is harassed by other passengers